# Energetics and the evolution of human brain size

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**Title:** Energetics and the evolution of human brain size: no gut-brain trade-off in mammals

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## Abstract

The human brain stands out among mammals by being unusually large. The Expensive Tissue Hypothesis[1] explains its evolution by proposing a trade-off between the size of the brain and that of the digestive tract, which is smaller than expected for a primate of our body size. Although this hypothesis is widely accepted, empirical support to date is equivocal. Here, we test it in a sample of 100 mammal species, including 23 primates, with matching brain size and organ mass data. We found that, controlling for fat-free body mass, brain size is not negatively correlated with the mass of the digestive tract or any other expensive organ, thus refuting the Expensive Tissue Hypothesis. Nonetheless, consistent with the existence of energy trade-offs with brain size we find that the size of brains and adipose depots are negatively correlated in mammals, suggesting that encephalization and fat storage are compensatory strategies to buffer against starvation. However, these two strategies can be combined if fat storage does not unduly hamper locomotor efficiency. We propose that human encephalization was made possible by a combination of stabilization of energy inputs and a redirection of energy from locomotion, growth and reproduction.

## Text

Brains are energetically expensive[2]. The human brain is about three times larger than that of our closest living relative, the chimpanzee, and thus requires much more energy. However, relative whole-body energy consumption rates of individuals at rest are about equal in the two species[3],

which raises the question of how humans manage to cover the energetic requirements of their much enlarged brains. One of the best-known attempts to solve this central riddle of human evolution is the Expensive Tissue Hypothesis, proposed by Aiello and Wheeler in 1995[1]. It postulates an evolutionary trade-off (though obviously not an immediate physiological one) between the size of the brain and that of the digestive tract in anthropoid primates. Thus, if other processes have reduced a species' energetic needs of digestion, it should be able to evolve a relatively larger brain. It has therefore been suggested that early hominins evolved larger brains as a diet shift towards more meat[1], cooked food and underground tubers[4] gradually allowed for a smaller digestive tract.

The proposed trade-off would gain much plausibility as a general principle if it would be confirmed in other mammals. As stressed by Aiello *et al.*[5], empirical support for a negative correlation across anthropoid primate species was weak from the beginning (see Suppl. Info. section 1 for a re-analysis), and subsequent comparative studies in other taxa remained ambiguous, with positive support in fish[6], but not in bats or birds[7,8]. Yet, this highly intuitive idea has found broad acceptance in palaeoanthropology[9] and many other fields[10-12], and is fuelling public discussions about the optimal human diet. Thus, a proper empirical test of the Expensive Tissue Hypothesis across a broad array of taxa was urgently needed, but has so far not been conducted due to lack of morphological data, nor has there been an examination of the broader trade-offs amongst other expensive organs predicted by an extension of this hypothesis[7].

Here, we examine the presence of correlated evolution of organ sizes in a new dataset of the mass of various visceral organs (heart, lungs, stomach, intestines, kidneys, spleen and liver) and associated brain size for 100 mammal species, including 23 primate species (see Suppl. Data). Dissections followed a strict protocol and were all conducted by one of the authors (A.N.). We

excluded individuals that were immature, emaciated, pregnant, or exhibited visible organ pathologies from analysis.

In this analysis, it is crucial to control for body size. The usual measure taken for this, body mass, is highly affected by variation in the size of adipose depots, which may confound or even reverse the direction of correlations among organs (Suppl. Fig. 2, Suppl. Table 4b). Here, we therefore used fat-free body mass as the best proxy for body size. All analyses took phylogenetic relatedness into account (Suppl. Fig. 3). The sample size of 100 species yields a power of 0.8 for these analyses, which was determined a priori using a published dataset of 39 mammal species (see Methods).

Contrary to the predictions of the Expensive Tissue Hypothesis, we found no negative correlations between the relative size of the brain and the digestive tract, other expensive organs or their combined sum among mammals or within non-human primates, controlling for fat-free body mass, even though statistical power was sufficient to detect these negative correlations if they existed (see Table 1). We also did not find any trade-offs amongst other expensive organs (Fig. 1). These results therefore refute the Expensive Tissue Hypothesis as a general principle to explain the interspecific variation of relative brain size in mammals. In our view, this finding reduces the plausibility of the argument that human encephalization was made possible by a reduction of the digestive tract[1,5].

Energy trade-offs with other tissues that are less expensive but very abundant[7], may nonetheless explain part of brain size variation. For instance, adipose depots make up an appreciable proportion of body mass in some mammals[13]. Although not metabolically expensive, adipose tissue has an energetic cost because it has to be carried around and may increase predation-induced mortality (see Suppl. Info. 3.7.). Fat stores enable animals to cope with periods of reduced food

intake and thus act as a physiological buffer against starvation. On the other hand, relatively large brains have also been proposed to act as cognitive buffers against starvation[14,15]. It is therefore possible that encephalization and fat storage are complementary strategies to buffer against starvation. In our mammal sample, there is indeed a negative correlation between brain size and the size of fat stores, controlling for fat-free body mass (Table 2 and Suppl. Info. 3.1.), with the exception of primates (but see Suppl. Info. 3.6.). This negative relationship becomes stronger if potential error variation is removed, for instance by analysing only wild-caught females (Fig. 2 and Suppl. Info. 3.4.). The strongest trade-off between fat storage and brain size evolution is expected in taxa that exhibit high cost of transport for increased whole body mass, such as climbing or flying mammals and birds. The only animals that can easily combine both strategies of fat storage and brain enlargement may be those that do not face increased cost of transport for increased whole body mass, e.g. aquatic mammals or large bipeds[16]. However, more detailed studies of seasonal variation in body mass are needed to investigate which conditions or lifestyles favour one or the other, or a combination of both strategies.

Where does refuting the Expensive Tissue Hypothesis leave us with respect to explaining the evolution of the much enlarged human brain? Although there are various cognitive benefits to increased brain size[17], empirical evidence shows that a focus on the energy costs of growing and maintaining brain tissue helps to explain the interspecific variation in brain size[18]. This approach has recently been synthesized in a general energy-based framework[19], which incorporates earlier ideas on energetic aspects of brain size evolution[1,5,18]. Figure 3 depicts the two possible pathways enabling increased encephalization from a given ancestral state: additional or stabilized energy inputs, and redirection of energy from other functions. Here we apply this framework to develop hypotheses for the remarkable increase of brain size during the evolution of the genus *Homo*.

Larger brains are sometimes paid for by a permanent increase in net energy intake of an organism, as indexed by its basal metabolic rate (BMR), as shown by the positive correlation between BMR and brain size in a large sample of placental[20] and marsupial mammals[21]. This was confirmed in the present data set, where we could control for fat-free body mass (N=64, PGLS, brain size as response, fat-free body mass and body mass associated with BMR measurements as covariates, effect of BMR: lambda=0.96, p=0.026, beta=0.24). We humans exhibit the BMR expected for a mammal or primate of our body mass, but because we have much larger adipose depots (about 14-26% in healthy adults[22]) than chimpanzees and bonobos (about 3-10%[23]), human BMR relative to fat-free body mass is appreciably higher than theirs[24]. Therefore, if extant apes are representative of the last common ancestor, brain enlargement during human evolution was partially paid for through a permanent increase in net energy intake.

Starting with Early Pleistocene *Homo,* this increase could have come from any of the three sources listed in Figure 3. First, they improved diet quality as indicated by increased consumption of meat and bone marrow[1] and by tool-assisted food processing, at one point including cooking[4]. Second, despite having moved into highly seasonal habitats[9] they reduced temporal fluctuations in energy budgets by cognitive buffering[25], which is also known for other primates[15] and birds[14]. Third, provisioning and food sharing probably arose with the adoption of cooperative breeding and substantial meat acquisition among the earlier representatives of the genus *Homo*[4,26]. Comparative research suggests that such energy subsidies for reproducing females and dependent offspring can support increased brain size[19,21].

The second pathway to brain enlargement is increased energy allocation to the brain by savings on other expensive functions, although the Expensive Tissue Hypothesis for organs is no longer supported. One likely trade-off could be found between brain size and the costs of

113 locomotion. The efficient form of bipedal locomotion that arose with the transition from
114 australopithecines to early *Homo*[27] could have lead to major reductions in energy expenditure in two
115 ways. On one hand, its low costs in comparison with the climbing and quadrupedal locomotion of
116 nonhuman apes[28] should have lowered daily energy expenditure on locomotion[7], and on the other
117 hand, bipedalism may reduce the effect of increased weight due to adipose depots on the energy
118 costs of locomotion (Suppl. Info. 3.7). A second potential trade-off would be the one between brain
119 size and production, comprising both growth and reproductive effort, which has been demonstrated
120 for mammals[19,29]. Beginning with early *Homo* our lineage has increased brain size and reduced the
121 pace of life history[30], but nonetheless increased birth rates due to cooperative breeding.

122 In sum, we do not claim unique processes operating exclusively in human evolution. All
123 these processes are known to operate among mammals in general. We propose that during human
124 evolution improved diet quality, allomaternal subsidies, cognitive buffering, reduced locomotion
125 costs and reduced allocation to production all operated simultaneously, thus enabling the
126 extraordinary brain enlargement in our lineage.

127

## Methods

**Power analysis:** To estimate the sample size needed to detect a correlation between brain size and digestive tract mass in mammals controlling for fat-free body mass, we used an independent dataset of 39 mammal species[31]. In a multiple regression, digestive tract mass has a standard error of the residual error sigma of 0.343, and a raw effect size delta of 0.096. Therefore, for a level of significance of alpha =0.05, the sample size required to achieve a power of 0.8 is 103 species. We thus aimed at collecting data from more than 100 mammal species.

**Specimens:** 454 specimens of 133 mammal species were obtained from various sources and dissected following a strict protocol (Suppl. Info. 2.) by one author (A.N.). Visceral organs (kidneys, spleen, liver, stomach, intestines, heart and lungs) were separated, cleaned, emptied, and immediately weighed. As skulls had to be preserved intact, cranial capacity was determined using the seed filling method[32], and converted into an estimate of brain mass by multiplying it with 1.036[33]. Specimens were excluded from analyses if they were juvenile or subadult, emaciated, pregnant, previously stored in formalin or alcohol, had visible pathologies of the organs (such as tumors or internal parasites), a broken neurocranium, unknown body mass prior to dissection, or if the organ measurements were incomplete. Our final sample included 191 specimens from 100 species, with a bias towards larger orders and especially carnivores and primates (see Suppl. Info. 3.2. for species and family coverage and an additional analysis on subfamily level). Species values were obtained by calculating the average of male and female specimens (see Suppl. Info. 3.4. for an analysis of sex-specific and wild/captive subsamples). Intestine mass was defined as the sum of ileum, caecum and colon mass, and digestive tract mass as the sum of stomach and intestines mass. Basal metabolic rate (BMR) data of the species of our sample or of closely related taxa were taken from the literature. Data and sources are listed in Suppl. Data.

**Adipose depots:** For 45 species in our sample, adipose depots of the whole body were measured directly. For the other 55 species, only abdominal adipose depots were measured, from which we calculated a proxy of total adipose depots by scaling the abdominal depots mass with a factor 3.419. This scaling factor was derived from a comparison of the two measurements for 292 individuals for which body mass and one of the two adipose depots measurements was available (Suppl. Fig. 1). Alternatively, the total mass of adipose depots was calculated from abdominal mass using a prediction equation derived from nine specimens for which both measurements were available (results shown in Suppl. Info. 3.3.). Fat-free body mass was calculated as whole body mass minus total adipose depots mass.

**Statistical analyses:** All variables were log-transformed and phylogenetic regressions were run using pglmEstLambda in the CAIC[34] package in R[35]. This function uses the phylogenetic generalized least-squares (PGLS) method, estimating lambda as an index of the amount of phylogenetic autocorrelation in the data. If lambda is 0, species values are phylogenetically independent and the analysis is equivalent to a species means least-squares regression. If lambda is close to 1, the phylogenetic signal implies that trait evolution follows Brownian motion, and the analysis is equivalent to the classic method of calculating independent contrasts. If analyses yielded unstable estimates of lambda due to the small sample size within orders (lambda not significantly different from both 0 and 1), we additionally ran the analyses with lambda set to 0 or 1. The models included brain mass as response, body size as covariate and organ mass as effect.

Visceral organs, the brain and adipose depots are part of the same body, and therefore autocorrelation effects could be suspected to influence our results. Two methods to remove these effects are reported in the Suppl. Info. 3.5., and the results corroborate our findings. Analyses were

done both using the total sample of 100 species and the subsample with total adipose depot mass of 45 species.

**Whole body mass vs. fat-free body mass:** Traditionally, *whole body mass* has been used for controlling for body size effects in comparative analyses. However, this measure is highly affected by variation in the size of adipose depots and using it to control for body size may have an effect on the correlation between organs. Even if two species have a similar *fat-free body mass* and body composition, large adipose depots in one species result in organs that seem relatively smaller in comparison to those of a species with smaller adipose depots. Therefore, correlations between organs are mostly positive if we control for *whole body mass*. This bias is expected to disappear if *fat-free body mass* is used to control for body size effects (Suppl. Fig. 2).

These relationships were confirmed by our analyses. Brain-organ correlations were mostly positive, if *whole body mass* was included in the model (Suppl. Tables 4 and 5). Controlling for *fat-free body mass* instead of whole body mass reduced or eliminated this bias in most groups, with the notable exception of primates, where positive correlations between organs persist, and brain size is not negatively related to adipose depots mass. We argue (Suppl. Info. 3.6.) that these discrepancies are due to a combination of error and peculiar captivity effects in foregut fermenting primates, and that primates would follow the general mammal trend if more complete data were available.

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## Supplementary Information

### Excel file

Supplementary Data

The file Navarrete_SupplData.xls displays the compiled dataset of organ mass and metabolic data for 100 mammal species.

### PDF file

Supplementary Information

The file Navarrete_SupplInfo.pdf contains an evaluation of the original anthropoid dataset used to establish the Expensive Tissue Hypothesis, Supplementary Methods, and Supplementary Results and Discussion.

## Acknowledgements

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## Author contributions

K.I. and C.v.S designed the project. A.N. performed the pilot study and collected the data. A.N. and K.I. performed the analyses and all three authors wrote the manuscript.

## Author information

Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the article at www.nature.com/nature. Correspondence and requests for materials should be addressed to A.N. (a.navarrete@aim.uzh.ch) or K.I. (kisler@aim.uzh.ch).

## Tables

**Table 1**: Pair-wise phylogenetic least-squares regression (PGLS) between brain volume and other organ masses, controlling for fat-free body mass. Statistical details and the results of the N=45 species subsample are listed in Suppl. Info. 3.1.

| | **Mammals (N=100)** | | **Primates (N=23)** | |
|---|---|---|---|---|
| Organ | β | p-value | β | p-value |
| Heart | 0.15 | 0.13 | **0.65** | **0.007** |
| Lungs | -0.03 | 0.73 | 0.44 | 0.07 |
| Kidneys | 0.01 | 0.92 | 0.34 | 0.08 |
| Liver | -0.02 | 0.84 | 0.20 | 0.3 |
| Digestive tract | 0.16 | 0.06 | **0.48** | **0.005** |
| *Stomach* | **0.15** | **0.042** | 0.17 | 0.19 |
| *Intestines* | 0.11 | 0.15 | **0.41** | **0.008** |
| Spleen | -0.02 | 0.60 | 0.15 | 0.13 |
| Visceral organs | 0.05 | 0.64 | **0.50** | **0.029** |
| Adipose depots | **-0.07** | **0.017** | -0.01 | 0.92 |

## Figure legends

**Figure 1**: Correlations between the masses of visceral organs, brains and adipose depots in a sample of 100 mammal species, controlling for phylogenetic relationships and fat-free body mass. Statistical details are listed in the Suppl. Info. 3.1.

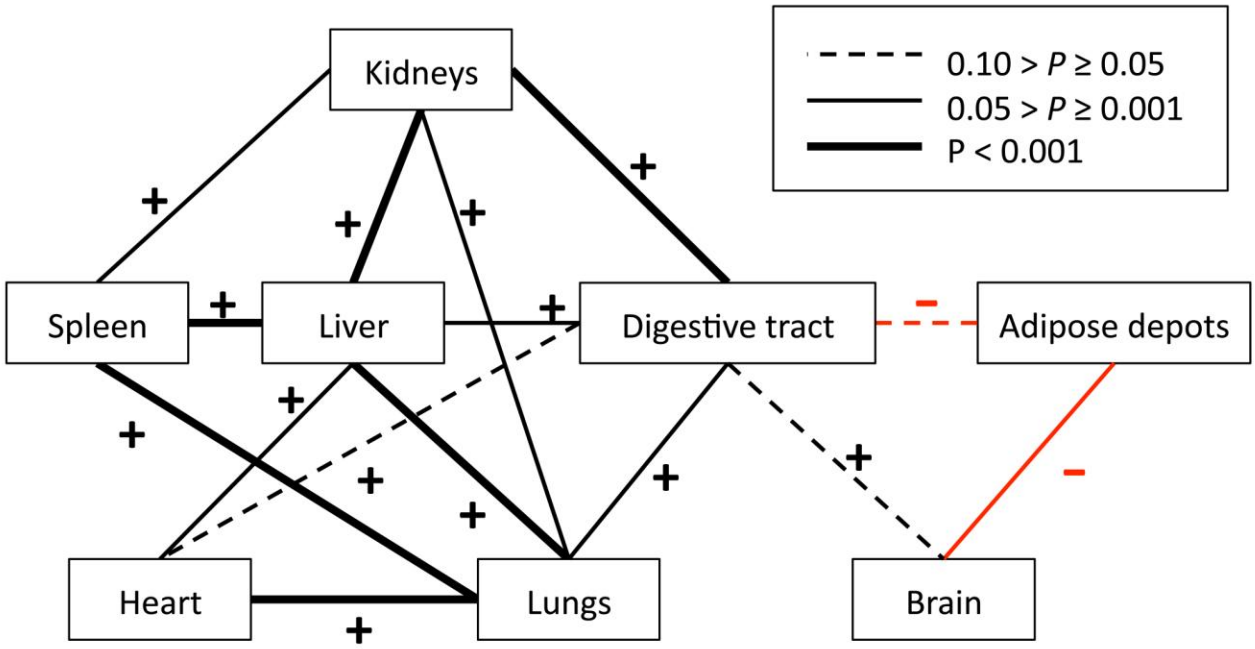
Navarrete_fig1.jpg

**Figure 2**: Regression of residual brain mass vs. residual adipose depots mass in wild-caught female mammals, controlling for fat-free body mass (raw data: residual ln(adipose depots) = 0 - 1.21*residual ln(brain mass); N=28 species, p=0.006, $r^2$=0.258; PGLS: $\lambda$=1.00, $\beta$=-0.12, t-value=-3.42, p=0.002).

Navarrete_fig2.jpg

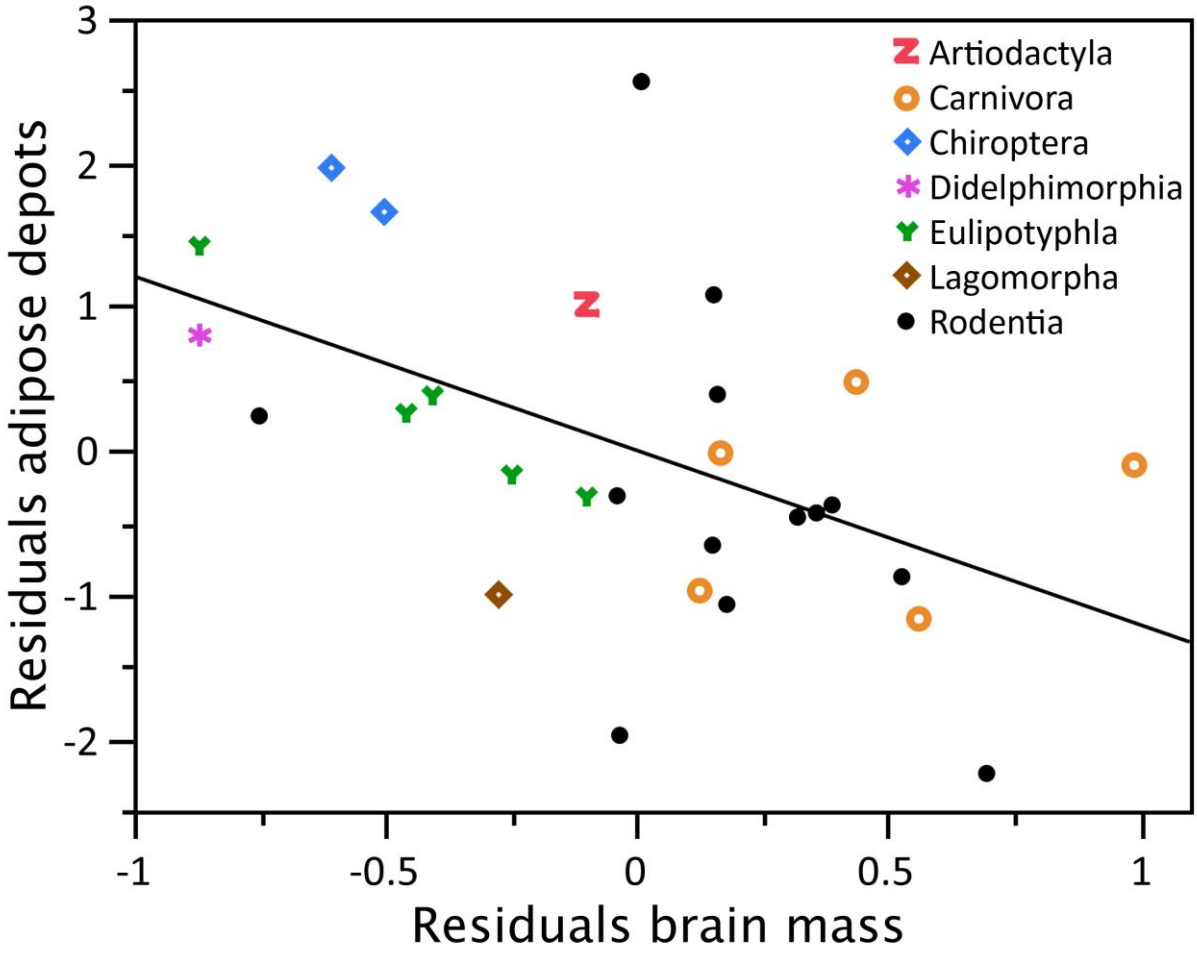
**Figure 3**: The Expensive Brain framework[19] proposes complementary pathways for an adaptive increase in relative brain size. First, brains can get larger when energy inputs are stabilized on a higher level (higher total metabolic turnover[20]) through an increase in mean dietary quality (e.g. more animal fat and protein in early *Homo*[4,22,24]), energy subsidies from other individuals (e.g. cooperative breeding, allomaternal care[19,21]) or by reducing fluctuations in energy inputs (e.g. cognitive solutions[15] including culture). Second, at constant total energy intake, energy allocation to other functions may be reduced, such as locomotion (e.g. efficient bipedalism[27,28]) or production (e.g. slower life history pace[30]).

Navarrete_fig3.jpg


0.10 > P ≥ 0.05
0.05 > P ≥ 0.001
P < 0.001
Kidneys
Spleen
Liver
Digestive tract
Adipose depots
Heart
Lungs
Brain

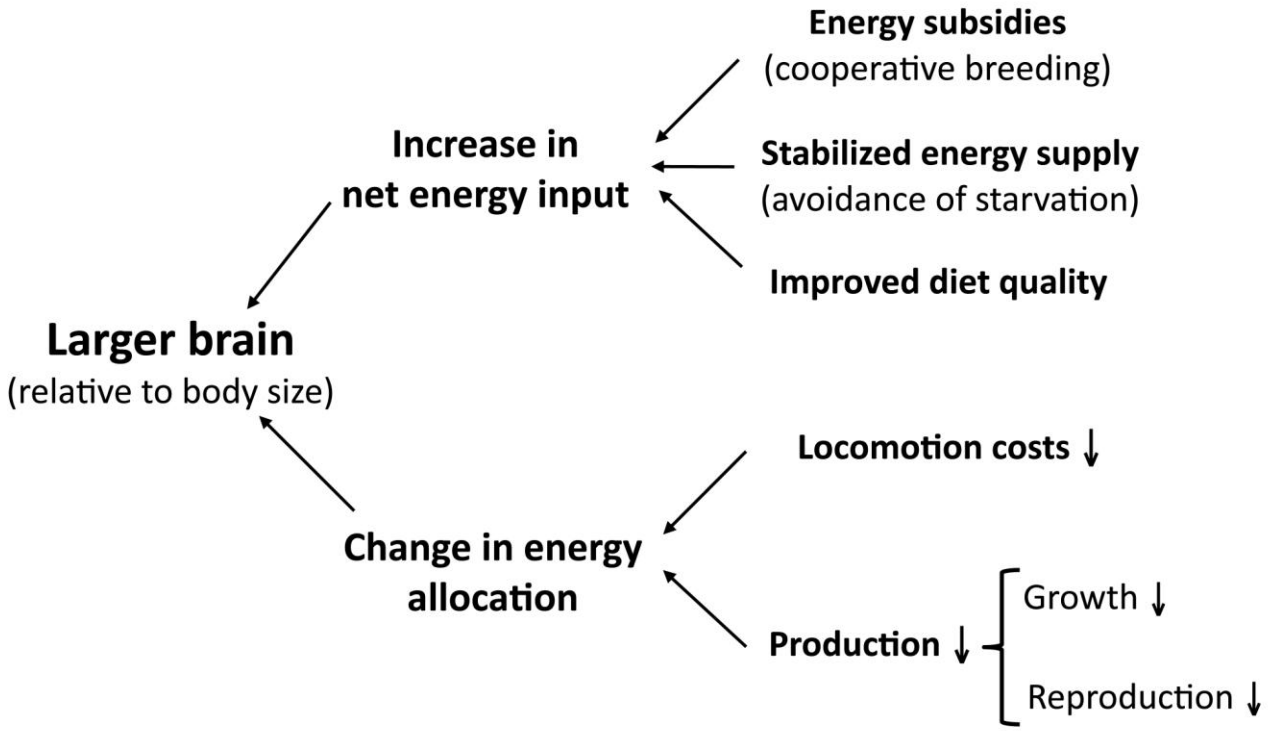
320

321


Residuals adipose depots
Residuals brain mass
3
2
1
0
-1
-2
-1
-0.5
0
0.5
1
Artiodactyla
Carnivora
Chiroptera
Didelphimorphia
Eulipotyphla
Lagomorpha
Rodentia

322

323


Energy subsidies
(cooperative breeding)
Increase in
net energy input
Stabilized energy supply
(avoidance of starvation)
Improved diet quality
Larger brain
(relative to body size)
Locomotion costs ↓
Change in energy
allocation
Production ↓
Growth ↓
Reproduction ↓

# Energetics and the evolution of human brain size: no gut-brain trade-off in mammals

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## Supplementary Information

**Content**



**Other Supplementary Files**

Navarrete_SupplData.xls

Note for all tables: λ: ML-estimate of lambda, β: PGLS estimate of the effect size. If the lambda value is not significantly different from both 0 and 1 (italics), both classic independent contrasts and raw species regressions are shown additionally. P values <0.05 are shown in bold face.

**Supplementary Information 1: Evaluation of the original anthropoid dataset to establish the Expensive Tissue Hypothesis**

## Introduction

In addition to compiling and analyzing our own dataset, we also conducted a detailed evaluation of the original study that supported the Expensive Tissue Hypothesis in anthropoid primates[1]. Their original analysis was based on combining the digestive tract and body mass data from Chivers and Hladik[36] with brain size and body mass data from Harvey and Clutton-Brock[37] for anthropoid primates. The Chivers dataset included individual mass and surface area measurements from several components of the digestive tract (stomach, ileum, caecum and colon) as well as body mass in a sample of 157 mammalian specimens, including 37 primate species (the published data were corrected for a layout error, and complemented by the full list of measurements made available by D. Chivers to R.D. Martin and L. Aiello). Aiello and Wheeler analyzed the anthropoid species from this dataset and published their species averages several years later[5] (Suppl. Table 2). The original analysis of Aiello and Wheeler yielded a negative correlation between brain size and digestive tract mass (the sum of stomach, ileum, caecum and colon mass), controlling for the effect of body mass ($N = 18$, $r = -0.69$, $P < 0.001$). This negative correlation persisted when *Homo sapiens* was excluded from the sample[5] ($n = 17$, $r$ -0.62, $P = 0.007$).

In this evaluation, we use the Chivers and Hladik dataset to test the Expensive Tissue Hypothesis, making full use of current phylogenetic methodology[34] and more accurate sex-specific brain volume and body mass data that have become available in recent years[15,32].

## Methods

Individual measurements of digestive tract mass were taken from the full Chivers dataset, after the exclusion of individuals suspected to be emaciated or immature. Brain volume and body mass from wild-caught adult primates were obtained from published sources[15,32] and additional measurements by J. van Woerden (pers. comm.).

The original study correlated brain mass with gut mass, i.e. digestive tract mass, described as the sum of the masses of stomach, ileum, caecum and colon. In this evaluation, we correlated brain mass with stomach mass, intestine mass (described as the sum of ileum, caecum and colon) and digestive tract mass. Because brains and digestive tract measures were obtained from

different specimens, a major challenge is to deal with the variability in body mass within species and the resulting error of estimating the relative size of organs. In order to obtain an optimum correspondence between digestive tract and brain specimens, we included only adults that were not emaciated as compared to average body mass values for the respective sex (body mass more than 75% of the average mass). To preclude confounding effects of body mass dimorphism between the sexes, we adhered to the following rationale: first, we calculated the averages for the digestive tract variables for each species, while recording whether the average included only females, only males or both sexes. Second, brain mass was paired to the digestive tract values as follows: for species with no sexual dimorphism in body mass (less than 10% difference between males and females), we took the average brain mass for both sexes; otherwise, we took the average brain mass for the same sex or the whole species depending on the sex of the individuals included in the digestive tract averages. Our final sample included N=23 anthropoid species and N=2 strepsirrhines (Suppl. Table 2).

All variables were log-transformed and phylogenetic regressions (PGLS) were run using pglmEstLambda in the CAIC package[34] in R[35] with the consensus tree from the 10kTrees project[38]. As the small sample size yielded unstable estimates of lambda in some cases (lambda not significantly different from either 0 or 1), we also ran all analyses with lambda set to 0 (raw data) or 1 (classic independent contrasts). The phylogenetic least-squares regression model included both body masses and the digestive tract mass as independent variables and brain mass as the dependent variable.

**Results and discussion**

In contrast to the original result of Aiello and Wheeler[1], our revised sample did not yield any significantly negative correlations between brain and one of the digestive tract variables or the combined digestive tract mass (Suppl. Table 1). Results did not differ according to whether phylogenetic information was taken into account or not, and whether the two strepsirrhine species were included or not.

There are various reasons for the discrepancy between these results and the originally reported negative correlation. First, the Harvey dataset reported some brain size values that were not confirmed for some species in subsequent reports, and sometimes reported only male values without mentioning this fact. Second, sexual size dimorphism affects body mass more than brain mass[39], which may confound analyses where sex is not taken into account. Third, brain size data

have become available for more platyrrhine species in recent years, reducing the bias toward catarrhine species in the original analysis. Fourth, we excluded clearly emaciated individuals of the Chivers dataset in our analysis. In conclusion, matching the best available brain and body mass data with the Chivers dataset does not yield support for the Expensive Tissue Hypothesis in anthropoid primates.

**Supplementary Table 1:** Correlations between brain mass residuals and the residuals of mass of stomach, intestines and digestive tract (sum of stomach and intestines).

| | | **A: dataset from Aiello and Wheeler, excluding *Homo sapiens*** | | | **B: revised dataset** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **Digestive tract mass** | | | **Stomach mass** | | | **Intestine mass** | | **Digestive tract mass** | |
| | Sample | N | λ | p-value | N | λ | p-value | λ | p-value | λ | p-value |
| PGLS | Primates | | | | 25 | 0 | 0.24 (-) | 0 | 0.17 (+) | 0 | 0.86 (+) |
| | Anthropoidea | 17 | 1 | **0.0001 (-)** | 23 | 0 | 0.23 (-) | 0 | 0.16 (+) | 0 | 0.94 (+) |
| IC | Primates | | | | 25 | 1 | 0.82 (-) | 1 | 0.90 (+) | 1 | 0.93 (-) |
| | Anthropoidea | 17 | 1 | **0.0001 (-)** | 23 | 1 | 0.91 (-) | 1 | 0.65 (+) | 1 | 0.83 (+) |
| GLM | Primates | | | | 25 | 0 | 0.24 (-) | 0 | 0.17 (+) | 0 | 0.86 (+) |
| | Anthropoidea | 17 | 0 | **0.004 (-)** | 23 | 0 | 0.23 (-) | 0 | 0.16 (+) | 0 | 0.94 (+) |

PGLS: phylogenetic least-squares methods, IC: classic independent contrasts (lambda set to 1), GLM: linear model of logged species data (lambda set to 0). (+) indicates a positive correlation, (-) indicates a negative correlation. Significant p-values are shown in bold face.

**Supplementary Table 2:** The two datasets based on the digestive tract mass data from Chivers and Hladik[36].

| | | A: Dataset used by Aiello and Wheeler | | | | B: Revised dataset | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Digestive tract data[36] | | Brain data[37] | | Digestive tract data[36] | | | | | Brain data[32] | | | | | | |
| | | | | | | | | | | | Female | | Male | | | Adjusted sex | |
| Group | Species | BM | DT | BM | Brain | $N_{ind}$ | BM | St | Int | DT | BM | Brain | BM | Brain | Dim | Sex | BM | Brain |
| Str | *Galago alleni* | | | | | 1f | 250 | 3 | 11 | 14 | 269 | 5 | 277 | 6 | 1.03 | m/f | 273 | 6 |
| Str | *Galagoides demidoff* | | | | | 1m | 60 | 1 | 1 | 2 | 75 | 3 | 76 | 3 | 1.02 | m/f | 76 | 3 |
| Pla | *Saguinus mystax* | | | | | 1m | 560 | 2 | 21 | 23 | 584 | 10 | 629 | 10 | 1.08 | m/f | 607 | 10 |
| Pla | *Alouatta belzebul* | | | | | 3f/1m | 5050 | 94 | 274 | 368 | 5520 | 51 | 5525 | 55 | 1.00 | m/f | 5523 | 53 |
| Pla | *A. seniculus* | 4450 | 360 | 7250 | 58 | 1m | 6150 | 116 | 325 | 441 | 5210 | 55 | 6668 | 55 | 1.28 | m | 6668 | 55 |
| Pla | *Callicebus moloch* | | | | | 2m | 1165 | 7 | 32 | 39 | 887 | 17 | 935 | 18 | 1.05 | m/f | 911 | 17 |
| Pla | *Cebus apella* | 2890 | 110 | 2480 | 71 | 1f | 2000 | 16 | 86 | 102 | 2489 | 64 | 3383 | 69 | 1.36 | f | 2489 | 64 |
| Pla | *Lagothrix lagotricha* | 8050 | 362 | 6300 | 96 | 1f/1m | 8050 | 93 | 269 | 362 | 7020 | 89 | 7280 | 89 | 1.04 | m/f | 7150 | 89 |
| Pla | *Saimiri sciureus* | 740 | 39 | 665 | 24 | 1f/1m | 990 | 6 | 39 | 45 | 743 | 24 | 860 | 24 | 1.16 | m/f | 802 | 24 |
| Cat | *Cercopithecus cephus* | 3338 | 120 | 3500 | 64 | 1f/2m | 3567 | 26 | 102 | 127 | 2880 | 61 | 4290 | 66 | 1.49 | m/f | 3585 | 63 |
| Cat | *C. neglectus* | 4081 | 254 | 5480 | 71 | 1f/1m | 7595 | 61 | 212 | 273 | 4130 | 61 | 8048 | 67 | 1.95 | m/f | 6089 | 64 |
| Cat | *C. nictitans* | | | | | 1m | 6500 | 61 | 157 | 218 | 4260 | 67 | 6670 | 73 | 1.57 | m | 6670 | 73 |
| Cat | *Erythrocebus patas* | 11650 | 280 | 7800 | 107 | 1m | 11650 | 54 | 226 | 280 | 6500 | 89 | 12400 | 97 | 1.91 | m | 12400 | 97 |
| Cat | *Macaca fascicularis* | 3175 | 149 | 5000 | 69 | 1f/2m | 4400 | 38 | 167 | 205 | 3518 | 61 | 5360 | 65 | 1.52 | m/f | 4439 | 63 |
| Cat | *Mandrillus sphinx* | | | | | 1f | 12300 | 123 | 641 | 764 | 12800 | 136 | 45000 | 159 | 3.52 | f | 12800 | 136 |
| Cat | *Colobus polykomos* | 7662 | 380 | 9400 | 77 | 2f | 8465 | 190 | 173 | 363 | 6709 | 71 | 10600 | 78 | 1.58 | f | 6709 | 71 |
| Cat | *Nasalis larvatus* | 15880 | 598 | 15100 | 94 | 1m | 15880 | 357 | 241 | 598 | 9730 | 85 | 19392 | 99 | 1.99 | m | 19392 | 99 |
| Cat | *Presbytis melalophos* | 6781 | 254 | 6650 | 80 | 3f/3m | 6537 | 122 | 134 | 256 | 6567 | 61 | 6554 | 72 | 1.00 | m/f | 6561 | 66 |
| Cat | *P. rubicunda* | 6350 | 171 | 6300 | 93 | 1m | 6350 | 105 | 66 | 171 | 6221 | 69 | 6310 | 75 | 1.01 | m/f | 6266 | 72 |
| Cat | *Trachypithecus cristatus* | 6850 | 433 | 8350 | 64 | 2f | 6145 | 224 | 149 | 372 | 6060 | 58 | 6728 | 62 | 1.11 | f | 6060 | 58 |
| Cat | *T. obscurus* | 7580 | 315 | 7400 | 68 | 1f/2m | 7170 | 182 | 133 | 314 | 6765 | 59 | 7347 | 64 | 1.09 | m/f | 7056 | 62 |
| Cat | *Symphalangus syndactylus* | 9300 | 490 | 10750 | 122 | 1f | 11340 | 146 | 390 | 536 | 11295 | 124 | 11453 | 126 | 1.01 | m/f | 11374 | 125 |
| Cat | *Hylobates pileatus* | | | | | 1f | 7260 | 56 | 238 | 294 | 5470 | 85 | 5500 | 95 | 1.01 | m/f | 5485 | 90 |
| Cat | *Hylobates lar** | 5200 | 188 | 5500 | 108 | | | | | | | | | | | | | |
| Cat | *Pongo pygmaeus* | 64819 | 1591 | 53000 | 413 | 1f | 56250 | 185 | 1095 | 1280 | 36948 | 338 | 80643 | 413 | 2.18 | m/f | 58796 | 375 |
| Cat | *Gorilla gorilla* | | | | | 1m | 236000 | 595 | 4396 | 4991 | 71500 | 434 | 141500 | 528 | 1.98 | m | 141500 | 528 |
| Cat | *Homo sapiens*** | 60800 | 1107 | 65000 | 1300 | | | | | | | | | | | | | |

All values are in grams. Stre: strepsirrhine, Pla: platyrrhines, Cat: catarrhines, BM: body mass, DT: digestive tract, St: stomach, Int: intestines, $N_{ind}$: number of individuals used in the average, Dim: index of sexual dimorphism in body mass ($BM_{male}/BM_{female}$). m/f: average of male and female values.

* *Hylobates lar*: excluded because the specimens were "fixed", which may influence organ masses.

** Testing the Expensive Tissue Hypothesis as a general pattern to explain the *Pan-Homo* distinction requires that *Homo sapiens* is excluded from the comparison. The *Homo* values in the Aiello and Wheeler sample were taken from Ashoff et al.[40], presumably because the body mass value of the Chivers individuals is very low (45kg).

**Supplementary Information 2: Supplementary Methods**

This section contains a dissection protocol, the calculation of total adipose depots mass from abdominal adipose depots mass (Suppl. Figure 1), a rationale for how to control for the effect of body size (Suppl. Figure 2), and the phylogenetic tree (Suppl. Figure 3).

**Specimens**

Cadavers were collected from various museums, zoos and donors: Naturhistorisches Museum Basel, Naturhistorisches Museum Fribourg, Muséum d'Histoire Naturelle Genève, Muséum d'Histoire Naturelle Neuchâtel, Zoologisches Museum der Universität Zürich, Zoo Zürich, Knies Kinderzoo Rapperswil, Igelzentrum Zürich, Wildpark Langenberg, Dr. Marcus Clauss, Alexander Schweiger, Dr. Anna Lindholm, Dr. Carsten Schradin, Heinz Galli (all CH), Naturhistorisches Museum Mainz, Staatliches Museum für Naturkunde Stuttgart, Wilhelm and Helga Klemens, Elke Kissel (all DE), Zoo Antwerpen (NL), Royal Museum of African Fauna Tervuren (BE), National Museums of Scotland (UK), Hungarian Natural History Museum (HU), and the Field Museum of Natural History (USA).

**Dissection protocol**

Information about sex, age, origin, time and cause of death of the specimens was collected when available. Museum staff performed skinning and bone preparation if the specimens were to be prepared for their collections. Specimens from the National Museums of Scotland were prepared for dissection by G. Hantke by removing the bulk of all visceral organs, and keeping them frozen in a sealed plastic bag until A. Navarrete performed the dissections. All other cadavers were dissected by A. Navarrete.

Preparations: Frozen specimens were allowed to thaw (2h for small specimens, overnight for large specimens) and external moisture on the skin was removed using a hair dryer. The total body mass was weighed when the body temperature equaled ambient temperature. The specimens were skinned and the skin was weighed. To avoid desiccation, the organs were put onto a wet paper towel immediately after removal. For weighing, individual organs were put onto small sheets of aluminum (small specimens) or into plastic containers (larger specimens), and net weights determined. All weights were recorded in grams.

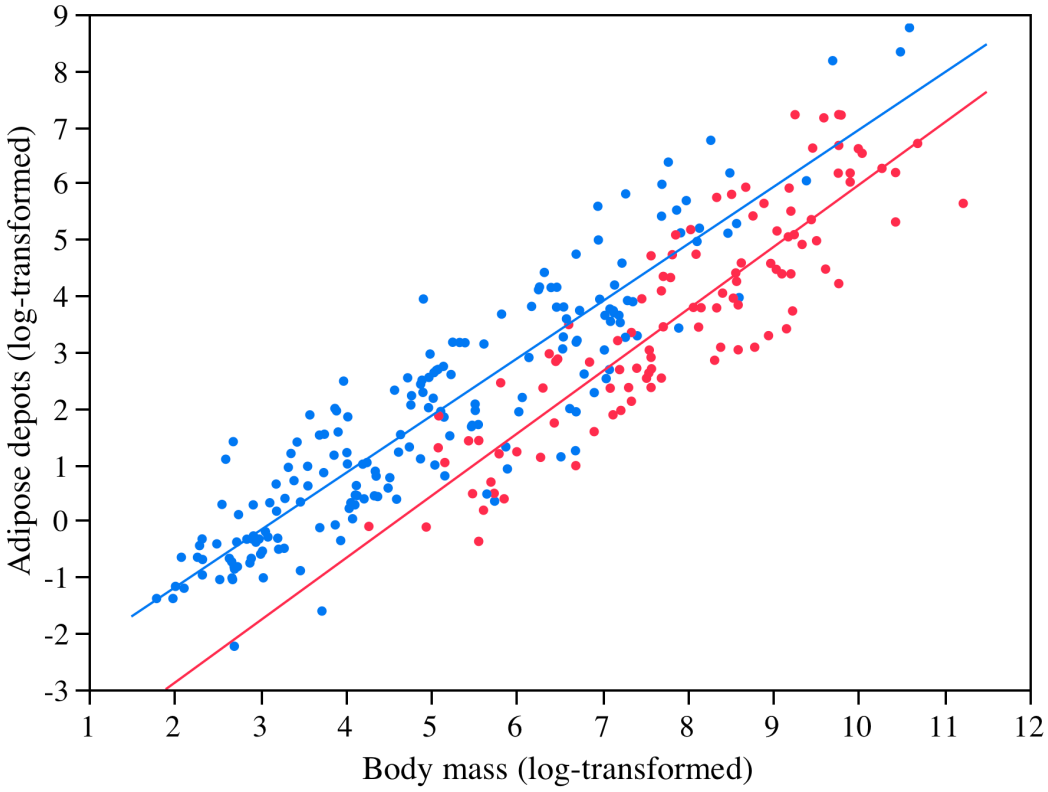
Abdominal cavity: The testes were removed in male specimens. The abdominal cavity was opened with a ventral cut from sternum to pubis and two transverse cuts along the distal end

of the rib cage. The spleen was removed. The small intestine was shifted aside, and the kidneys and additional male sexual structures (seminal vesicles) were cut off and removed. The adrenal glands were separated from the kidneys. The digestive tract was removed cutting the esophagus at the level of the diaphragm and cutting the anus and, in females, the vulva. The female sexual organs were removed. The liver and pancreas were removed. The digestive tract (stomach and intestines) was cleaned from connective and adipose tissue, laid on millimeter paper and photographed. Stomach, ileum, caecum and colon were separated, weighed a first time, cut open to remove contents, washed, dried with a paper towel after washing to remove excess water and weighed empty a second time. The other abdominal organs were weighed.

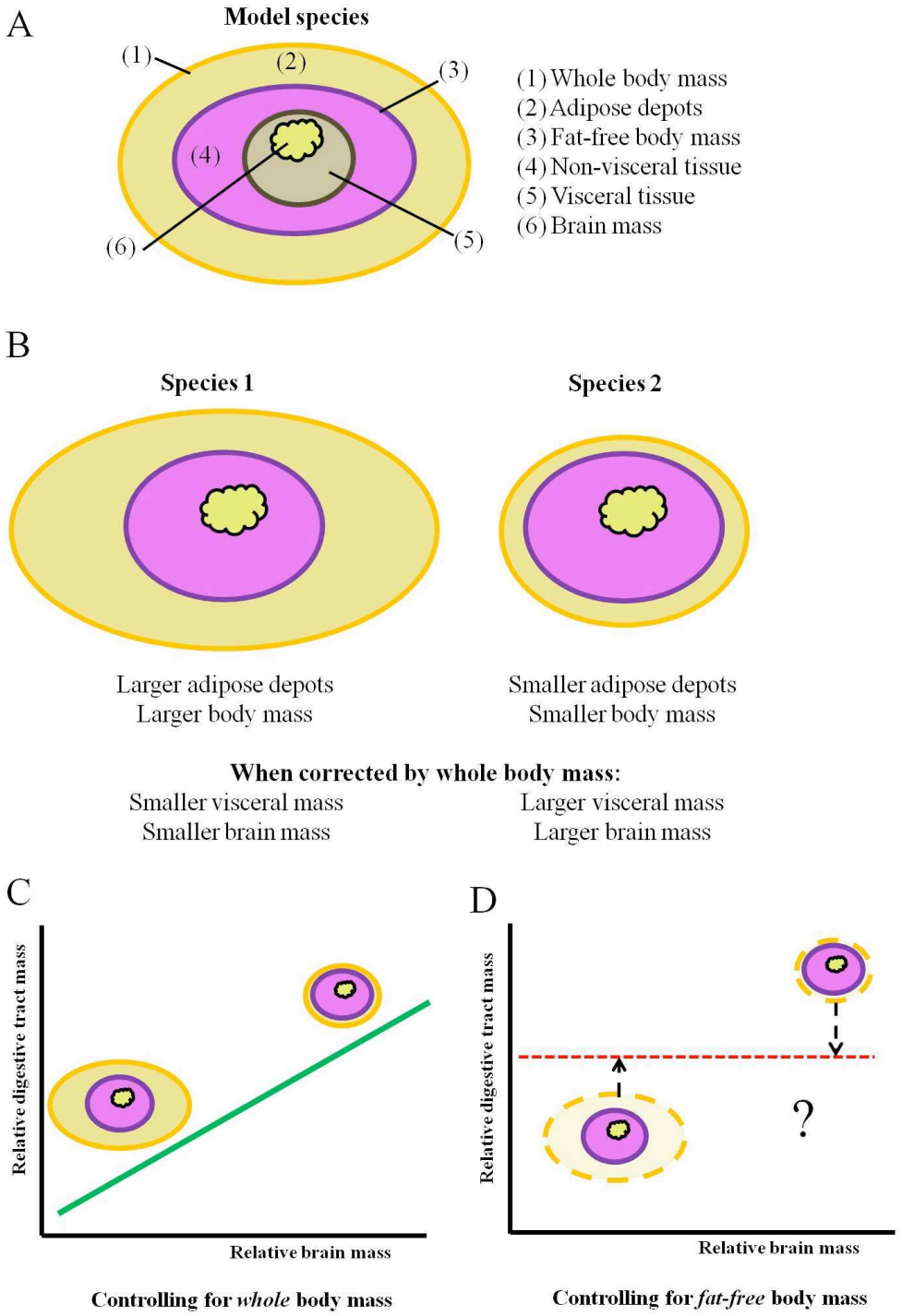
Thoracic cavity: The diaphragm was cut open following the inner rib cage line. Trachea and esophagus were cut above the sternum, and connective tissue was loosened to allow the thoracic organs to be pulled out distally. The heart was separated, opened and the chambers were cleaned of blood coagulations by rinsing. The lungs were separated by cutting the bronchi. The thoracic organs were weighed.

Adipose depots: During dissection, visible subcutaneous and intermuscular accumulations of adipose depots were continuously removed and put in a separate container. Adipose depots were removed from the walls of the abdominal and thoracic cavities, and from between the visceral organs. The total adipose depots were weighed. For 45 species in our sample, adipose depots of the whole body were measured directly. For the other 55 species, only abdominal adipose depots were measured, from which we calculated a proxy of total adipose depots by scaling the abdominal depots mass with a factor 3.419. This scaling factor was derived from a comparison of the two measurements for all individuals for which body mass and one of the two adipose depots measurements was available (Suppl. Figure 1). Fat-free body mass was calculated as whole body mass minus total adipose depots mass. The rationale on the usage of fat-free body mass to control for differences in body size between species is illustrated in Suppl. Figure 2.

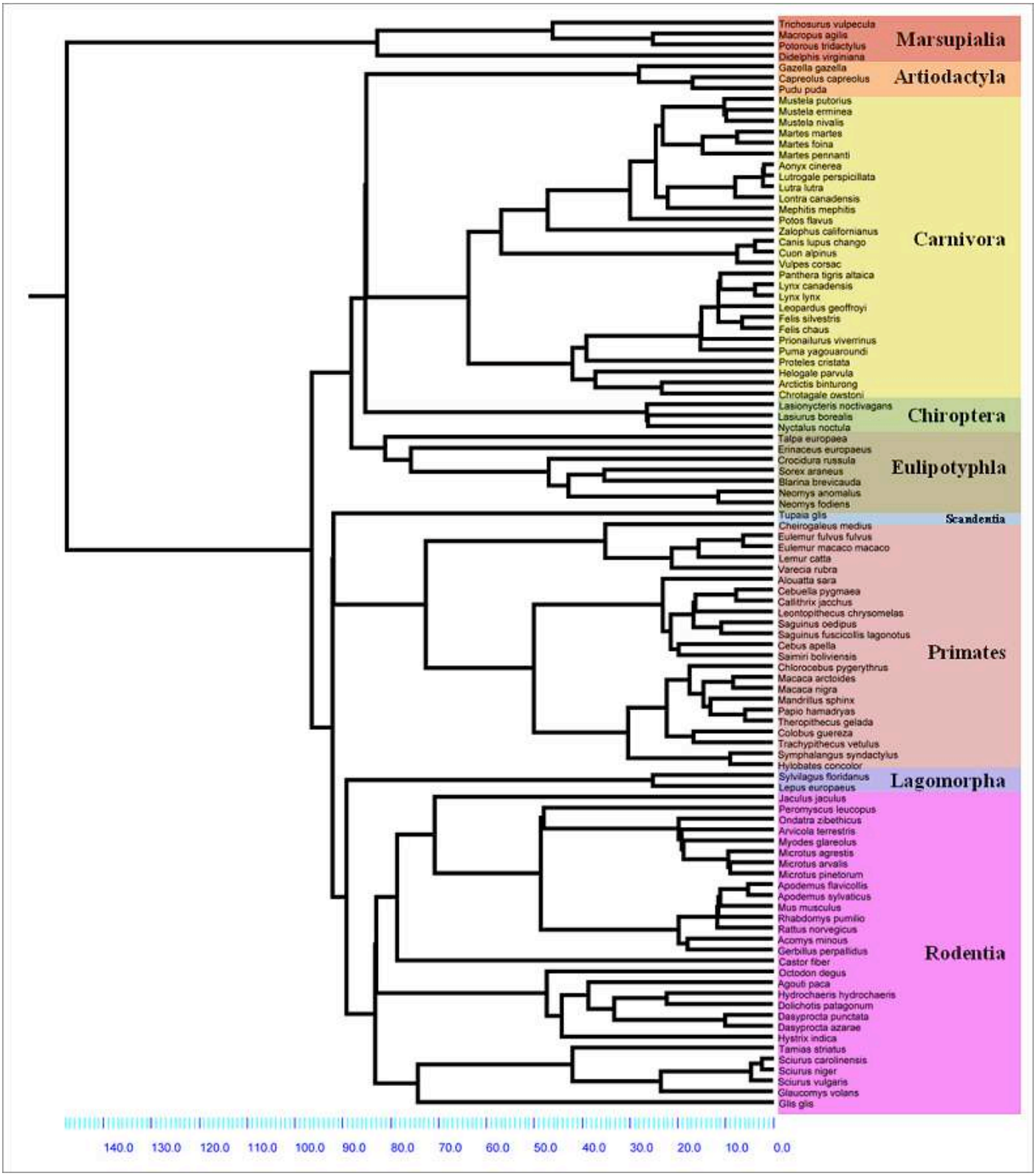
Skeletal measures: Some weeks to months later, the specimens were skeletonized (but not degreased), and the bones were dried and weighed. The cranial capacity was determined using the seed filling method[32], and converted into an estimate of brain mass by multiplying the volume with 1.036[33].




**Supplementary Figure 1**: Regression of adipose depots mass on body mass for 292 specimens. The slopes of the least-squares regression of total adipose depots (blue symbols) vs. body mass (ln(total fat): -3.233+1.017 ln(body mass), N=188) and the least-squares regression of abdominal adipose depots (red symbols) vs. body mass (ln(abdominal fat): -5.103+1.106 ln(body mass), N=104) did not differ significantly from each other. Thus, a common slope of 1.0401 was fitted to both subsamples (ln(abdominal fat): -4.578 +1.0401 ln(body mass), N=104; ln(total fat): -3.348+1.0401 ln(body mass), N=188), and the scaling factor was derived from the intercept difference, 1/exp(-4.5775+3.3482)=3.419. Using fat-free body mass would yield a very similar correction factor of 3.46. An alternative method is described in Section 3.3.




**Supplementary Figure 2**: The rationale for controlling for body size by using fat-free body mass. A species is depicted by its body composition (A). Two species may have the same fat-free body mass, but different amounts of adipose depots (B). Controlling for whole body mass yields positive correlations between organ masses (C). Only controlling for fat-free body mass allows us to detect a possible trade-off between the sizes of different organs (D).




**Supplementary Figure 3:** Phylogenetic tree of the 100 mammal species in our sample, mainly from Bininda-Emonds et al.[41]. Distances are given in million years before present. As the phylogenetic generalized least-squares method (PGLS) requires a completely resolved

phylogeny, polytomies were resolved using various sources. Within Chiroptera, *Lasiurus* and *Nyctalus* are more closely related to each other than to *Lasionycteris* according to Volleth and Heller[42]. Within Carnivora, polytomies in the Lutrinae group were resolved using Koepfli et al.[43]. Within Rodentia, the phylogeny of Cricetidae follows Robovský et al.[44], the one of Muridae follows Lecompte et al.[45], and the distance between Cricetidae and Muridae was taken from Michaux et al.[46]. Within Caviidae, distances were taken from Rowe and Honeycutt[47] and Veniaminova et al.[48]. Distances within Primates were modified following Arnold et al.[38].

**Supplementary Information 3: Supplementary results and discussion**

### 3.1. Extended results, including the N=45 species subsample

This section contains the correlation matrix for all organs used for Figure 2 in the main text (Suppl. Table 3), full statistics for the results shown in Table 1 in the main text (Suppl. Table 4), and additional results for the 45-species sample with known total adipose depots mass (Suppl. Table 5).

**Supplementary Table 3:** Pair-wise correlation matrix including brain, visceral organs, and adipose depots mass. All correlations are controlled for fat-free body mass and calculated by PGLS.

| | Heart | Lungs | Kidneys | Liver | Digestive tract | *Stomach* | *Intestines* | Spleen | Adipose depots |
|---|---|---|---|---|---|---|---|---|---|
| Brain | β = 0.15<br>P = 0.13 | β = -0.03<br>P = 0.73 | β = 0.01<br>P = 0.92 | β = -0.02<br>P = 0.85 | β = 0.16<br>P = 0.06 | β = 0.15<br>**P = 0.042** | β = 0.11<br>P = 0.15 | β = -0.02<br>P = 0.60 | β = -0.07<br>**P = 0.017** |
| Heart | | β = 0.63<br>**P<0.0001** | β = 0.15<br>P = 0.13 | β = 0.18<br>**P = 0.035** | β = 0.16<br>P = 0.09 | β = 0.08<br>P = 0.27 | β = 0.12<br>P = 0.13 | β = 0.05<br>P = 0.15 | β = -0.03<br>P = 0.32 |
| Lungs | | | β = 0.27<br>**P=0.004** | β = 0.32<br>**P<0.0001** | β = 0.18<br>**P = 0.042** | β = 0.06<br>P = 0.36 | β = 0.14<br>P = 0.07 | β = 0.13<br>**P<0.0001** | β = -0.003<br>P = 0.93 |
| Kidneys | | | | β = 0.45<br>**P<0.0001** | β = 0.29<br>**P = 0.002** | β = 0.06<br>P = 0.40 | β = 0.28<br>**P=0.0002** | β = 0.11<br>**P = 0.003** | β = 0.005<br>P = 0.88 |
| Liver | | | | | β = 0.30<br>**P = 0.005** | β = 0.06<br>P = 0.43 | β = 0.26<br>**P = 0.004** | β = 0.15<br>**P<0.0001** | β = -0.01<br>P = 0.74 |
| Digestive tract | | | | | | β = 0.53<br>**P<0.0001** | β = 0.81<br>**P<0.0001** | β = 0.05<br>P = 0.19 | β = -0.07<br>P = 0.07 |
| *Stomach* | | | | | | | β = 0.39<br>**P<0.0001** | β = 0.04<br>P = 0.37 | β = -0.03<br>P = 0.55 |
| *Intestine* | | | | | | | | β = 0.04<br>P = 0.39 | β = -0.11<br>**P = 0.013** |
| Spleen | | | | | | | | | β = 0.11<br>P = 0.24 |

**Supplementary Table 4**: Pair-wise phylogenetic least-squares regression (PGLS) between brain and other organ masses (N = 100 species), controlling for a) fat-free body mass, and b) whole body mass.

| **a)** | **Including *fat-free body mass* as covariate** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | PGLS | | | | | | Independent contrasts (λ = 1) | | | Raw data (λ = 0) | | |
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value | β | t-value | p-value | β | t-value | p-value |
| **Mammals** | **N=100** | | | | | | | | | | | |
| Heart | 0.918 | <0.0001 | 0.001 | 0.15 | 1.51 | 0.13 | | | | | | |
| Lungs | 0.928 | <0.0001 | 0.010 | -0.03 | -0.35 | 0.73 | | | | | | |
| Kidneys | 0.921 | <0.0001 | 0.004 | 0.01 | 0.10 | 0.92 | | | | | | |
| Liver | 0.923 | <0.0001 | 0.005 | -0.02 | -0.19 | 0.84 | | | | | | |
| Digestive tract | 0.943 | <0.0001 | 0.007 | 0.16 | 1.89 | 0.06 | | | | | | |
| *Stomach* | 0.934 | <0.0001 | 0.005 | 0.15 | 2.06 | **0.042** | | | | | | |
| *Intestine* | 0.940 | <0.0001 | 0.007 | 0.11 | 1.45 | 0.15 | | | | | | |
| Spleen | 0.929 | <0.0001 | 0.008 | -0.02 | -0.53 | 0.60 | | | | | | |
| Visceral organs | 0.922 | <0.0001 | 0.0020 | 0.05 | 0.46 | 0.64 | | | | | | |
| Adipose depots | 0.938 | <0.0001 | 0.029 | -0.07 | -2.42 | **0.017** | | | | | | |
| **Primates** | **N=23** | | | | | | | | | | | |
| Heart | 0.347 | 1.00 | 0.033 | 0.65 | 2.99 | **0.007** | | | | | | |
| Lungs | 0.703 | *0.13* | *0.25* | 0.44 | 1.93 | 0.07 | 0.44 | 1.97 | 0.06 | 0.51 | 1.97 | 0.06 |
| Kidneys | 0.717 | *0.05* | *0.69* | 0.34 | 1.86 | 0.08 | 0.24 | 1.27 | 0.22 | 0.31 | 1.46 | 0.16 |
| Liver | 0.664 | *0.18* | *0.16* | 0.20 | 1.06 | 0.30 | 0.14 | 0.73 | 0.48 | 0.27 | 1.29 | 0.21 |
| Digestive tract | 1.000 | *0.10* | *1.00* | 0.48 | 3.14 | **0.005** | | | | 0.5 | 2.79 | **0.011** |
| *Stomach* | 0.857 | *0.07* | *0.57* | 0.17 | 1.35 | 0.19 | 0.22 | 1.71 | 0.10 | 0.14 | 1.03 | 0.31 |
| *Intestine* | 1.000 | *0.10* | *1.00* | 0.41 | 2.95 | **0.008** | | | | 0.41 | 2.57 | **0.018** |
| Spleen | 0.838 | 0.036 | 0.29 | 0.15 | 1.56 | 0.13 | | | | | | |
| Visceral organs | 0.663 | *0.17* | *0.31* | 0.50 | 2.35 | **0.029** | 0.51 | 2.43 | **0.025** | 0.57 | 2.46 | **0.023** |
| Adipose depots | 0.793 | *0.29* | *0.23* | -0.01 | -0.10 | 0.92 | -0.02 | -0.26 | 0.80 | -0.09 | -1.11 | 0.28 |
| **Carnivora** | **N=28** | | | | | | | | | | | |
| Heart | 0.000 | 1.00 | 0.0001 | -0.02 | -0.12 | 0.91 | | | | | | |
| Lungs | 0.000 | 1.00 | 0.003 | -0.16 | -1.05 | 0.31 | | | | | | |
| Kidneys | 0.000 | 1.00 | 0.001 | 0.050 | 0.33 | 0.74 | | | | | | |
| Liver | 0.000 | 1.00 | 0.0003 | -0.01 | -0.08 | 0.93 | | | | | | |
| Digestive tract | 0.000 | 1.00 | 0.0004 | 0.16 | 0.86 | 0.40 | | | | | | |
| *Stomach* | 0.000 | 1.00 | 0.0002 | 0.08 | 0.55 | 0.59 | | | | | | |
| *Intestine* | 0.000 | 1.00 | 0.0004 | 0.15 | 0.90 | 0.38 | | | | | | |
| Spleen | 0.000 | 1.00 | 0.001 | -0.03 | -0.52 | 0.61 | | | | | | |
| Visceral organs | 0.000 | 1.00 | 0.0003 | -0.09 | -0.41 | 0.69 | | | | | | |
| Adipose depots | 0.000 | 1.00 | <0.0001 | -0.04 | -0.90 | 0.38 | | | | | | |
| **Rodentia** | **N=29** | | | | | | | | | | | |
| Heart | 0.762 | 0.0004 | 0.001 | 0.23 | 1.90 | 0.07 | | | | | | |
| Lungs | 0.788 | 0.0002 | 0.003 | -0.02 | -0.16 | 0.87 | | | | | | |
| Kidneys | 0.776 | 0.0004 | 0.001 | -0.13 | -0.78 | 0.44 | | | | | | |
| Liver | 0.784 | 0.0002 | 0.002 | -0.10 | -0.70 | 0.49 | | | | | | |
| Digestive tract | 0.774 | 0.0038 | 0.0036 | -0.03 | -0.18 | 0.86 | | | | | | |
| *Stomach* | 0.805 | 0.0007 | 0.014 | 0.05 | 0.34 | 0.74 | | | | | | |
| *Intestine* | 0.769 | 0.003 | 0.002 | -0.04 | -0.29 | 0.78 | | | | | | |
| Spleen | 0.825 | <0.0001 | 0.008 | -0.08 | -1.43 | 0.16 | | | | | | |
| Visceral organs | 0.773 | 0.0007 | 0.001 | -0.10 | -0.48 | 0.63 | | | | | | |
| Adipose depots | 0.821 | <0.0001 | 0.010 | -0.08 | -1.97 | 0.06 | | | | | | |

**Supplementary Table 4 continued**:

| b) | Including *whole body mass* as covariate | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | PGLS | | | | | | Independent contrasts (λ = 1) | | | Raw data (λ = 0) | | |
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value | β | t-value | p-value | β | t-value | p-value |
| **Mammals** | **N=100** | | | | | | | | | | | |
| Heart | 0.905 | <0.0001 | 0.0002 | 0.22 | 2.32 | **0.022** | | | | | | |
| Lungs | 0.902 | <0.0001 | 0.0005 | 0.07 | 0.67 | 0.50 | | | | | | |
| Kidneys | 0.901 | <0.0001 | 0.0003 | 0.09 | 0.87 | 0.38 | | | | | | |
| Liver | 0.907 | <0.0001 | 0.0005 | 0.04 | 0.47 | 0.64 | | | | | | |
| Digestive tract | 0.940 | <0.0001 | 0.003 | 0.22 | 2.70 | **0.008** | | | | | | |
| *Stomach* | 0.928 | <0.0001 | 0.002 | 0.19 | 2.59 | **0.011** | | | | | | |
| *Intestine* | 0.938 | <0.0001 | 0.003 | 0.16 | 2.31 | **0.023** | | | | | | |
| Spleen | 0.912 | <0.0001 | 0.0010 | -0.01 | -0.29 | 0.77 | | | | | | |
| Visceral organs | 0.909 | <0.0001 | 0.0002 | 0.16 | 1.42 | 0.16 | | | | | | |
| Adipose depots | 0.932 | <0.0001 | 0.024 | -0.12 | -4.00 | **0.0001** | | | | | | |
| **Primates** | **N=23** | | | | | | | | | | | |
| Heart | 0.445 | 0.74 | 0.036 | 0.63 | 3.18 | **0.005** | | | | | | |
| Lungs | 0.759 | *0.10* | *0.28* | 0.45 | 2.01 | 0.06 | 0.60 | 2.31 | **0.032** | 0.47 | 2.16 | **0.043** |
| Kidneys | 0.756 | 0.028 | 0.070 | 0.34 | 1.75 | 0.10 | | | | | | |
| Liver | 0.737 | *0.09* | *0.14* | 0.21 | 1.12 | 0.28 | 0.17 | 0.91 | 0.38 | 0.33 | 1.52 | 0.14 |
| Digestive tract | 1.000 | *0.07* | *1.00* | 0.49 | 3.30 | **0.004** | | | | 0.55 | 3.06 | **0.006** |
| *Stomach* | 0.887 | 0.033 | 0.53 | 0.17 | 1.28 | 0.21 | | | | | | |
| *Intestine* | 1.000 | *0.06* | *1.00* | 0.42 | 3.22 | **0.004** | | | | 0.45 | 2.92 | **0.009** |
| Spleen | 0.775 | 0.009 | 0.36 | 0.18 | 1.95 | 0.07 | | | | | | |
| Visceral organs | 0.734 | *0.12* | *0.34* | 0.51 | 2.44 | **0.024** | 0.53 | 2.62 | **0.016** | 0.63 | 2.77 | **0.012** |
| Adipose depots | 0.781 | *0.26* | *0.21* | -0.07 | -0.91 | 0.37 | -0.06 | -1.01 | 0.32 | -0.15 | -1.87 | 0.08 |
| **Carnivora** | **N=28** | | | | | | | | | | | |
| Heart | 0.000 | 1.00 | 0.0001 | 0.06 | 0.41 | 0.69 | | | | | | |
| Lungs | 0.000 | 1.00 | 0.001 | -0.03 | -0.17 | 0.86 | | | | | | |
| Kidneys | 0.000 | 1.00 | 0.0002 | 0.14 | 0.91 | 0.37 | | | | | | |
| Liver | 0.000 | 1.00 | 0.0002 | 0.07 | 0.63 | 0.53 | | | | | | |
| Digestive tract | 0.000 | 1.00 | 0.0006 | 0.28 | 1.58 | 0.13 | | | | | | |
| *Stomach* | 0.000 | 1.00 | 0.0004 | 0.15 | 0.96 | 0.35 | | | | | | |
| *Intestine* | 0.000 | 1.00 | 0.0006 | 0.26 | 1.66 | 0.11 | | | | | | |
| Spleen | 0.000 | 1.00 | 0.003 | -0.03 | -0.55 | 0.59 | | | | | | |
| Visceral organs | 0.000 | 1.00 | 0.0001 | 0.13 | 0.63 | 0.53 | | | | | | |
| Adipose depots | 0.000 | 1.00 | <0.0001 | -0.11 | -2.09 | **0.047** | | | | | | |
| **Rodentia** | **N=29** | | | | | | | | | | | |
| Heart | 0.732 | 0.001 | 0.0008 | 0.28 | 2.31 | **0.029** | | | | | | |
| Lungs | 0.754 | 0.0006 | 0.0006 | 0.05 | 0.35 | 0.73 | | | | | | |
| Kidneys | 0.754 | 0.0009 | 0.0006 | -0.03 | -0.17 | 0.86 | | | | | | |
| Liver | 0.755 | 0.0007 | 0.0008 | -0.07 | -0.43 | 0.66 | | | | | | |
| Digestive tract | 0.792 | 0.002 | 0.005 | 0.08 | 0.51 | 0.61 | | | | | | |
| *Stomach* | 0.809 | 0.001 | 0.026 | 0.11 | 0.74 | 0.46 | | | | | | |
| *Intestine* | 0.779 | 0.002 | 0.002 | 0.05 | 0.35 | 0.73 | | | | | | |
| Spleen | 0.804 | 0.0001 | 0.003 | -0.08 | -1.37 | 0.18 | | | | | | |
| Visceral organs | 0.762 | 0.0009 | 0.0006 | 0.03 | 0.12 | 0.90 | | | | | | |
| Adipose depots | 0.800 | <0.0001 | 0.007 | -0.11 | -2.67 | **0.013** | | | | | | |

**Supplementary Table 5**: Pair-wise phylogenetic least-squares regression (PGLS) between brain and other organ masses (N = 45 species), controlling for a) fat-free body mass, and b) whole body mass.

| **a)** | **Including *fat-free body mass* as covariate** | | | | | |
|---|---|---|---|---|---|---|
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
| **Mammals** | **N=45** | | | | | |
| Heart | 0.933 | <0.0001 | 0.05 | 0.18 | 1.06 | 0.29 |
| Lungs | 0.918 | <0.0001 | 0.024 | 0.003 | 0.02 | 0.99 |
| Kidneys | 0.917 | <0.0001 | 0.02 | 0.05 | 0.30 | 0.77 |
| Liver | 0.919 | <0.0001 | 0.019 | 0.05 | 0.37 | 0.71 |
| Digestive tract | 0.933 | <0.0001 | 0.08 | 0.11 | 0.74 | 0.46 |
| *Stomach* | 0.936 | <0.0001 | 0.10 | 0.16 | 0.99 | 0.33 |
| *Intestine* | 0.928 | <0.0001 | 0.049 | 0.07 | 0.53 | 0.60 |
| Spleen | 0.933 | <0.0001 | 0.06 | -0.04 | -0.92 | 0.36 |
| Visceral organs | 0.924 | <0.0001 | 0.024 | 0.12 | 0.58 | 0.57 |
| Adipose depots | 0.940 | <0.0001 | 0.14 | -0.13 | -3.52 | **0.001** |
| **Non-Rodentia** | **N=21** | | | | | |
| Heart | 0.987 | 0.001 | 0.86 | 0.04 | 0.14 | 0.89 |
| Lungs | 0.999 | 0.001 | 0.99 | 0.14 | 0.55 | 0.59 |
| Kidneys | 1.000 | 0.0006 | 1.00 | 0.32 | 1.12 | 0.28 |
| Liver | 1.000 | 0.0005 | 1.00 | 0.20 | 1.33 | 0.20 |
| Digestive tract | 0.981 | 0.002 | 0.80 | -0.02 | -0.09 | 0.93 |
| *Stomach* | 0.981 | 0.002 | 0.81 | 0.01 | 0.06 | 0.96 |
| *Intestine* | 0.981 | 0.002 | 0.80 | -0.04 | -0.14 | 0.89 |
| Spleen | 0.981 | 0.002 | 0.80 | 0.009 | 0.15 | 0.88 |
| Visceral organs | 1.000 | 0.0008 | 1.00 | 0.35 | 1.18 | 0.25 |
| Adipose depots | 0.917 | 0.0004 | 0.30 | -0.18 | -2.66 | **0.016** |
| **Rodentia** | **N=24** | | | | | |
| Heart | 0.646 | 0.07 | 0.001 | 0.53 | 2.65 | **0.015** |
| Lungs | 0.762 | 0.002 | 0.004 | 0.01 | 0.07 | 0.94 |
| Kidneys | 0.755 | 0.003 | 0.002 | -0.12 | -0.62 | 0.54 |
| Liver | 0.764 | 0.002 | 0.004 | -0.11 | -0.63 | 0.53 |
| Digestive tract | 0.799 | 0.006 | 0.023 | 0.08 | 0.43 | 0.67 |
| *Stomach* | 0.816 | 0.004 | 0.049 | 0.13 | 0.65 | 0.52 |
| *Intestine* | 0.783 | 0.005 | 0.01 | 0.04 | 0.25 | 0.80 |
| Spleen | 0.826 | 0.0003 | 0.023 | -0.09 | -1.47 | 0.16 |
| Visceral organs | 0.758 | 0.003 | 0.002 | -0.05 | -0.20 | 0.84 |
| Adipose depots | 0.829 | 0.0002 | 0.031 | -0.09 | -2.15 | **0.043** |

**Supplementary Table 5 continued**:

| **b)** | **Including *whole body mass* as covariate** | | | | | |
|---|---|---|---|---|---|---|
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
| **Mammals** | **N=45** | | | | | |
| Heart | 0.942 | <0.0001 | 0.09 | 0.33 | 1.98 | 0.054 |
| Lungs | 0.910 | <0.0001 | 0.009 | 0.15 | 0.89 | 0.38 |
| Kidneys | 0.906 | <0.0001 | 0.015 | 0.20 | 1.17 | 0.25 |
| Liver | 0.912 | <0.0001 | 0.01 | 0.12 | 0.93 | 0.36 |
| Digestive tract | 0.945 | <0.0001 | 0.14 | 0.25 | 1.72 | 0.09 |
| *Stomach* | 0.949 | <0.0001 | 0.22 | 0.32 | 2 | 0.05 |
| *Intestine* | 0.935 | <0.0001 | 0.07 | 0.17 | 1.36 | 0.18 |
| Spleen | 0.923 | <0.0001 | 0.035 | -0.04 | -0.77 | 0.45 |
| Visceral organs | 0.928 | <0.0001 | 0.022 | 0.33 | 1.64 | 0.11 |
| Adipose depots | 0.929 | <0.0001 | 0.11 | -0.18 | -4.46 | **<0.0001** |
| **Non-Rodentia** | **N=21** | | | | | |
| Heart | 1.000 | 0.002 | 1.00 | 0.25 | 0.94 | 0.36 |
| Lungs | 1.000 | 0.001 | 1.00 | 0.34 | 1.26 | 0.22 |
| Kidneys | 1.000 | 0.0006 | 1.00 | 0.53 | 1.77 | 0.09 |
| Liver | 1.000 | 0.0006 | 1.00 | 0.26 | 1.70 | 0.11 |
| Digestive tract | 0.993 | 0.003 | 0.94 | 0.16 | 0.6 | 0.56 |
| *Stomach* | 0.990 | 0.003 | 0.91 | 0.21 | 0.83 | 0.41 |
| *Intestine* | 0.991 | 0.003 | 0.92 | 0.10 | 0.44 | 0.66 |
| Spleen | 0.991 | 0.003 | 0.92 | 0.02 | 0.26 | 0.80 |
| Visceral organs | 1.000 | 0.0004 | 1.00 | 0.56 | 1.95 | 0.07 |
| Adipose depots | 0.891 | 0.0006 | 0.19 | -0.27 | -3.68 | **0.002** |
| **Rodentia** | **N=24** | | | | | |
| Heart | 0.604 | 0.11 | 0.001 | 0.60 | 3.14 | **0.005** |
| Lungs | 0.712 | 0.007 | 0.001 | 0.12 | 0.59 | 0.56 |
| Kidneys | 0.727 | 0.005 | 0.001 | -0.008 | -0.04 | 0.97 |
| Liver | 0.725 | 0.005 | 0.002 | -0.06 | -0.30 | 0.76 |
| Digestive tract | 0.825 | 0.004 | 0.036 | 0.20 | 1.14 | 0.27 |
| *Stomach* | 0.845 | 0.004 | 0.12 | 0.27 | 1.26 | 0.22 |
| *Intestine* | 0.796 | 0.004 | 0.012 | 0.13 | 0.86 | 0.40 |
| Spleen | 0.800 | 0.001 | 0.011 | -0.10 | -1.45 | 0.16 |
| Visceral organs | 0.746 | 0.004 | 0.002 | 0.10 | 0.41 | 0.69 |
| Adipose depots | 0.810 | 0.0004 | 0.023 | 0.80 | 13.65 | **<0.0001** |

### 3.2. Dataset composition

This section contains a description of the composition of the dataset (Suppl. Table 6), and additional results of a procedure to control for a potential bias in the sample (Suppl. Table 7).

The composition of our dataset in relation to the total existing numbers of mammal species and families is shown in Suppl. Table 6. Although our dataset covers less than 2% of all mammal species, about a quarter of all mammal families are represented in our sample. However, Carnivora and Primates are overrepresented at the species level in our sample, whereas many small orders are not covered.

**Supplementary Table 6:** Composition of the organ mass sample. Numbers of mammalian species are taken from Wilson and Reeder[49].

| | **Species** | | | **Families** | | |
|---|---|---|---|---|---|---|
| | All | in our sample | coverage [%] | All | in our sample | coverage [%] |
| **Marsupialia** | | | | | | |
| Didelphimorphia | 87 | 1 | 1.1 | 1 | 1 | 100.0 |
| Diprotodontia | 143 | 3 | 2.1 | 11 | 3 | 27.3 |
| other marsupials | 101 | 0 | 0 | 9 | 0 | 0 |
| **Monotremata** | 5 | 0 | 0 | 2 | 0 | 0 |
| **Placentalia** | | | | | | |
| Artiodactyla | 240 | 3 | 1.3 | 10 | 3 | 30.0 |
| Carnivora | 286 | 28 | 9.8 | 15 | 9 | 60.0 |
| Chiroptera | 1116 | 3 | 0.3 | 18 | 1 | 5.6 |
| Erinaceomorpha | 24 | 1 | 4.2 | 1 | 1 | 100.0 |
| Lagomorpha | 92 | 2 | 2.2 | 3 | 1 | 33.3 |
| Primates | 376 | 23 | 6.1 | 15 | 8 | 53.3 |
| Rodentia | 2277 | 29 | 1.3 | 33 | 11 | 33.3 |
| Scandentia | 20 | 1 | 5.0 | 2 | 1 | 50.0 |
| Sorcimorpha | 428 | 6 | 1.4 | 4 | 2 | 50.0 |
| other mammals | 221 | 0 | 0 | 29 | 0 | 0 |
| **Total** | 5195 | 100 | 1.9 | 124 | 30 | 24.2 |

While phylogenetic methods are quite suitable to accommodate grade shifts in the data, an imbalance in the sample in combination with a different relationship within a specious taxon from that in other taxa, may still affect the results. One option to control for a possible bias is to look at large groups separately, which we did in Suppl. Tables 4 and 5. In general, the correlations are retained within the large orders, with the exception of primates (see Section 3.6).

Another option is to resample a better-balanced subset of the data, accepting the reduced sample size. We did this by selecting one species from each subfamily according to data quality (sample size, wild > captive, females > males, total adipose depots measured). Our final sample included 51 species. The significantly negative correlation between brain size and adipose depots mass persists in this subsample, although the p-value is slightly higher (Suppl. Table 7).

**Supplementary Table 7:** Pair-wise phylogenetic least-squares regression (PGLS) between brain and other organ masses (N = 51 species, one per subfamily), controlling for fat-free body mass.

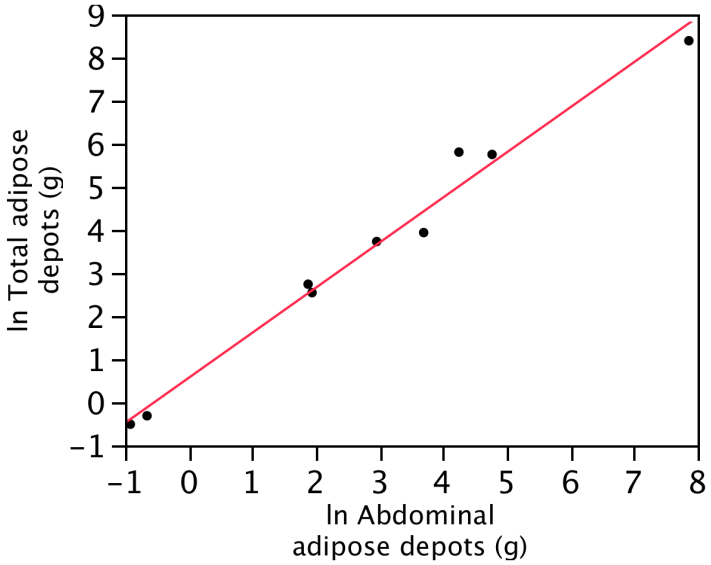
| **Organ** | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
|---|---|---|---|---|---|---|
| Heart | 0.936 | <0.0001 | 0.46 | 0.08 | 0.59 | 0.56 |
| Lungs | 0.929 | <0.0001 | 0.42 | 0.02 | 0.13 | 0.90 |
| Kidneys | 0.959 | <0.0001 | 0.56 | 0.25 | 1.69 | 0.10 |
| Liver | 0.943 | <0.0001 | 0.51 | 0.07 | 0.56 | 0.58 |
| Digestive tract | 0.929 | <0.0001 | 0.42 | 0.01 | 0.06 | 0.95 |
| *Stomach* | 0.933 | <0.0001 | 0.45 | -0.05 | -0.42 | 0.68 |
| *Intestine* | 0.941 | <0.0001 | 0.51 | 0.05 | 0.44 | 0.66 |
| Spleen | 0.920 | <0.0001 | 0.38 | -0.03 | -0.42 | 0.68 |
| Visceral organs | 0.941 | <0.0001 | 0.51 | 0.08 | 0.42 | 0.68 |
| Adipose depots | 0.904 | <0.0001 | 0.24 | -0.10 | -2.06 | **0.045** |

### 3.3. An alternative method to estimate total adipose depots mass

This section contains additional results on the relationship between brain size and adipose depots mass using an alternative method to estimate total adipose depots mass from abdominal depots mass (Suppl. Figure 4 and Suppl. Table 8).

As the variation in abdominal and total mass of adipose depots is rather large (cf. Suppl. Figure 1), we applied an alternative method to scale abdominal adipose depots to total adipose depots using the correlation between the two variables in 9 specimens for which we have both measurements (*Rattus norvegicus,* two *Mus musculus, Glis glis, Martes foina, Mephitis mephitis, Vulpes vulpes, Saimiri sciureus* and *Macaca fuscata*). A least-squares regression (Suppl. Figure 4) yields the following prediction equation:

ln(total adipose depots) = 0.564+1.047*ln(abdominal adipose depots)




**Supplementary Figure 4:** Regression of abdominal adipose depots vs. total adipose depots (N=9, $r^2$=0.982, P<0.0001).

From this, total adipose depots mass was calculated for all specimens for which only abdominal adipose depots mass was available. The resulting negative correlations between brain size and adipose depots mass are slightly stronger in all groups, most notably in all mammals combined (Suppl. Table 8). This result suggests that the found brain size – adipose depot trade-off is robust and does not rely on the details of the method used to scale the abdominal to total adipose depots mass.

**Supplementary Table 8:** Pair-wise phylogenetic least-squares regression (PGLS) between brain size and adipose depots mass, controlling for fat-free body mass, using an alternative method to calculate total adipose depots mass. Original results are duplicated from Suppl. Table 4a).

| | | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
|---|---|---|---|---|---|---|---|---|
| **All mammals** | Original | 100 | 0.938 | <0.0001 | 0.029 | -0.07 | -2.42 | **0.017** |
| | Alternative | 100 | 0.927 | <0.0001 | 0.003 | -0.09 | -2.07 | **0.002** |
| **Primates** | Original | 23 | 0.793 | *0.29* | *0.23* | -0.01 | -0.10 | 0.92 |
| | Alternative | 23 | 0.787 | *0.29* | *0.22* | -0.03 | -0.41 | 0.69 |
| **Carnivora** | Original | 28 | 0.000 | 1.00 | <0.0001 | -0.04 | -0.90 | 0.38 |
| | Alternative | 28 | 0.000 | 1.00 | 0.001 | -0.07 | -1.48 | 0.15 |
| **Rodentia** | Original | 29 | 0.821 | <0.0001 | 0.010 | -0.08 | -1.97 | 0.06 |
| | Alternative | 29 | 0.822 | <0.0001 | 0.010 | -0.08 | -2.02 | 0.054 |

### 3.4. Reducing error variation by splitting the sample into wild/captive, and male/female subsamples

This section contains additional results produced when the dataset was split into subsamples in an attempt to reduce error variation in the relationship between brain size and adipose depots mass (Suppl. Table 9).

Our organ mass sample contains specimens from a variety of living conditions, of both sexes, and from various habitats (cf. Suppl. Data), which may induce a large amount of error variation. By splitting our sample into subsets according to these groups, we can investigate whether the negative correlation between brain size and adipose depots mass is robust. We expect that the trade-off between fat storage and brain size is more pronounced in females than in males, because the former are more affected by energy constraints due to offspring production. As captivity effects are rather unpredictable (most animals gain weight in captivity, but only under good husbandry conditions), we expect that the trade-off is more pronounced in wild-caught specimens, although it may be argued that they are also more affected by seasonality effects on fat storage. Finally, storing fat may only be beneficial for survival if food availability in the habitat is seasonally variable. We therefore expect the trade-off to be more pronounced in species originating from temperate rather than from tropical habitats.

Results, shown in Suppl. Table 9, fully confirm these predictions. A significant negative correlation between brain size and adipose depots mass, controlling for fat-free body mass, is found in females, in wild-caught specimens, and in species of temperate origin, and is most pronounced in the subset of wild females. This result suggests that reducing error variation and

controlling for potentially confounding variables strengthens the evidence for a brain size-adipose depot trade-off.

**Supplementary Table 9:** Pair-wise phylogenetic least-squares regression (PGLS) between brain size and adipose depots mass split by habitat (temperate, tropical, both), sex (male, female), and provenience (captive, wild, no data), controlling for fat-free body mass. a) N=100 species, b) N=45 species.

**a)**

| Group | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
|---|---|---|---|---|---|---|---|
| **All specimens** | 100 | 0.938 | <0.0001 | 0.029 | -0.07 | -2.42 | **0.017** |
| Temperate | 52 | 0.933 | <0.0001 | 0.12 | -0.08 | -2.07 | **0.043** |
| Tropical | 43 | 0.934 | <0.0001 | 0.23 | -0.01 | -0.24 | 0.81 |
| Females | 57 | 0.934 | <0.0001 | 0.006 | -0.09 | -2.45 | **0.017** |
| Males | 69 | 0.905 | <0.0001 | 0.006 | -0.06 | -1.68 | 0.10 |
| Wild | 39 | 0.964 | <0.0001 | 0.39 | -0.12 | -2.74 | **0.010** |
| Captive | 59 | 0.823 | <0.0001 | 0.019 | -0.03 | -0.77 | 0.44 |
| Wild females | 28 | 1.000 | 0.0004 | 1.00 | -0.12 | -3.42 | **0.002** |

**b)**

| | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
|---|---|---|---|---|---|---|---|
| **All specimens** | 45 | 0.940 | <0.0001 | 0.14 | -0.13 | -3.52 | **0.001** |
| Temperate | 39 | 0.951 | <0.0001 | 0.24 | -0.1 | -2.37 | **0.023** |
| Tropical | 4 | | | | | | |
| Females | 30 | 1.000 | <0.0001 | 1.00 | -0.12 | -4.27 | **0.0002** |
| Males | 33 | 0.876 | 0.0002 | 0.006 | -0.12 | -2.13 | **0.041** |
| Wild | 35 | 0.951 | <0.0001 | 0.31 | -0.14 | -2.78 | **0.009** |
| Captive | 8 | 0.000 | 1.00 | 0.019 | 0.02 | 0.26 | 0.81 |
| Wild females | 25 | 1.000 | 0.0004 | 1.00 | -0.13 | -3.68 | **0.0013** |

### 3.5. Potential autocorrelation effects and compositional data analysis

This section contains results of an alternative procedure to control for the effect of body size (Suppl. Tables 10 and 11), and the results of compositional data analysis for the relationship between adipose depots mass and brain size (Suppl. Table 12).

A potential problem in the analysis of body composition data is the presence of autocorrelation effects, as the organs are part of the body mass which is used to control for size effects[50]. These effects are most pronounced when the parts comprise a large proportion of the whole body, but this is not the case in most of the correlations between brain size and one of the visceral organs in our sample. Furthermore, autocorrelation assumes that the total size of a sum of variables is strictly limited and thus constant. In the case of body mass, this assumption is overly conservative, because adding the size of some organ does not need to constrain the size of other organs. Nevertheless, to validate our results we applied two procedures to control for potential autocorrelation effects.

First, if we adjust our estimate of body size by controlling for *fat-free body mass minus brain mass and the respective organ mass* instead of just fat-free body mass, p-values remain largely similar, and in no case is the level of significance affected (Suppl. Table 10). The most critical result is the negative correlation between brain size and adipose depots mass. We checked for autocorrelation effects by controlling for fat-free body mass minus brain mass (Suppl. Table 11, analogous to the procedure for visceral organs shown in Suppl. Table 10). Results remain unchanged in the N=100 species sample, but significance is lost in the subsamples of the N=45 species sample.

Second, we applied compositional data analysis to control for potential autocorrelation effects in the brain size vs. adipose depots mass correlation (Suppl. Table 12). This method was developed for mathematical geology[51], and it has been applied to intraspecific body composition data before[52]. It takes into account that *n* parts of a whole are by necessity autocorrelated and transforms the values by projecting them onto a simplex of *n-1* dimensions. We used the function *acomp* for closed compositions in a logistic geometry, following a log-ratio approach and the isometric log-ratio transform *ilr*[53] from the package **compositions**[54] in R[35]. Thus, from the raw values of brain mass, adipose depots mass and the remaining body mass without brain and adipose depots, we obtained two transformed variables, which are no longer autocorrelated. We then tested their correlation with phylogenetic regression using *pglmEstLambda* from the package **CAIC** in R. Results yield very strong negative correlations in all subsamples.

**Supplementary Table 10**: Pair-wise phylogenetic least-squares regression (PGLS) between brain size and the mass of visceral organs, controlling for fat-free body mass minus brain mass and the respective organ mass. a) N=100 species, b) N=45 species.

| **a)** | **Including *fat-free body mass minus brain mass and organ mass* as covariate** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | PGLS | | | | | | Independent contrasts (λ = 1) | | | Raw data (λ = 0) | | |
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value | β | t-value | p-value | β | t-value | p-value |
| **Mammals** | **N=100** | | | | | | | | | | | |
| Heart | 0.918 | <0.0001 | 0.001 | 0.16 | 1.70 | 0.09 | | | | | | |
| Lungs | 0.926 | <0.0001 | 0.009 | -0.01 | -0.08 | 0.93 | | | | | | |
| Kidneys | 0.921 | <0.0001 | 0.004 | 0.03 | 0.30 | 0.77 | | | | | | |
| Liver | 0.923 | <0.0001 | 0.004 | 0.02 | 0.30 | 0.77 | | | | | | |
| Digestive tract | 0.945 | <0.0001 | 0.008 | 0.19 | 2.28 | **0.025** | | | | | | |
| *Stomach* | 0.936 | <0.0001 | 0.006 | 0.16 | 2.27 | **0.026** | | | | | | |
| *Intestine* | 0.942 | <0.0001 | 0.007 | 0.13 | 1.77 | 0.08 | | | | | | |
| Spleen | 0.929 | <0.0001 | 0.008 | -0.02 | -0.44 | 0.66 | | | | | | |
| Visc. organs | 0.923 | <0.0001 | 0.002 | 0.14 | 1.35 | 0.18 | | | | | | |
| **Primates** | **N=23** | | | | | | | | | | | |
| Heart | 0.325 | 1.00 | 0.032 | 0.68 | 3.12 | **0.005** | | | | | | |
| Lungs | 0.702 | *0.13* | *0.28* | 0.47 | 2.07 | 0.05 | 0.46 | 2.09 | 0.050 | 0.54 | 2.12 | **0.047** |
| Kidneys | 0.719 | 0.0495 | 0.07 | 0.35 | 1.94 | 0.07 | | | | | | |
| Liver | 0.670 | *0.17* | *0.17* | 0.24 | 1.27 | 0.22 | 0.17 | 0.91 | 0.38 | 0.31 | 1.50 | 0.15 |
| Digestive tract | 1.000 | *0.10* | *1.00* | 0.49 | 3.32 | **0.003** | | | | 0.53 | 3.01 | **0.007** |
| *Stomach* | 0.882 | *0.07* | *0.66* | 0.18 | 1.47 | 0.16 | 0.23 | 1.80 | 0.09 | 0.15 | 1.14 | 0.27 |
| *Intestine* | 1.000 | *0.09* | *1.00* | 0.33 | 2.59 | **0.018** | | | | 0.44 | 2.76 | **0.012** |
| Spleen | 0.845 | 0.034 | 0.31 | 0.16 | 1.61 | 0.12 | | | | | | |
| Visc. organs | 0.674 | *0.16* | *0.35* | 0.54 | 2.80 | **0.011** | 0.54 | 2.79 | **0.011** | 0.61 | 2.91 | **0.009** |
| **Carnivora** | **N=28** | | | | | | | | | | | |
| Heart | 0.000 | 1.00 | 0.0005 | 0.01 | 0.04 | 0.96 | | | | | | |
| Lungs | 0.000 | 1.00 | 0.014 | -0.11 | -0.76 | 0.45 | | | | | | |
| Kidneys | 0.000 | 1.00 | 0.007 | 0.080 | 0.55 | 0.59 | | | | | | |
| Liver | 0.000 | 1.00 | 0.0010 | 0.03 | 0.27 | 0.79 | | | | | | |
| Digestive tract | 0.000 | 1.00 | 0.0007 | 0.19 | 1.00 | 0.33 | | | | | | |
| *Stomach* | 0.000 | 1.00 | 0.0009 | 0.09 | 0.58 | 0.57 | | | | | | |
| *Intestine* | 0.000 | 1.00 | 0.0006 | 0.17 | 1.02 | 0.32 | | | | | | |
| Spleen | 0.000 | 1.00 | 0.013 | -0.02 | -0.44 | 0.67 | | | | | | |
| Visc. organs | 0.000 | 1.00 | 0.002 | 0.04 | 0.20 | 0.85 | | | | | | |
| **Rodentia** | **N=29** | | | | | | | | | | | |
| Heart | 0.760 | 0.0005 | 0.001 | 0.24 | 2.00 | 0.06 | | | | | | |
| Lungs | 0.786 | 0.0002 | 0.003 | -0.01 | -0.03 | 0.98 | | | | | | |
| Kidneys | 0.775 | 0.0005 | 0.001 | -0.12 | -0.66 | 0.51 | | | | | | |
| Liver | 0.783 | 0.0002 | 0.002 | -0.06 | -0.44 | 0.66 | | | | | | |
| Digestive tract | 0.779 | 0.0030 | 0.004 | -0.02 | 0.11 | 0.91 | | | | | | |
| *Stomach* | 0.808 | 0.0006 | 0.016 | 0.07 | 0.45 | 0.66 | | | | | | |
| *Intestine* | 0.773 | 0.002 | 0.002 | -0.01 | -0.04 | 0.97 | | | | | | |
| Spleen | 0.824 | <0.0001 | 0.007 | -0.08 | -1.39 | 0.18 | | | | | | |
| Visc. organs | 0.774 | 0.0006 | 0.001 | 0.01 | 0.05 | 0.96 | | | | | | |

**Supplementary Table 10 continued:**

| **b)** | **Including *fat-free body mass minus brain mass and organ mass* as covariate** | | | | | |
|---|---|---|---|---|---|---|
| Organ | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
| **Mammals** | **N=45** | | | | | |
| Heart | 0.945 | <0.0001 | 0.10 | 0.20 | 1.23 | 0.22 |
| Lungs | 0.930 | <0.0001 | 0.05 | 0.01 | 0.07 | 0.94 |
| Kidneys | 0.930 | <0.0001 | 0.043 | 0.04 | 0.22 | 0.83 |
| Liver | 0.930 | <0.0001 | 0.033 | 0.09 | 0.82 | 0.41 |
| Digestive tract | 0.936 | <0.0001 | 0.08 | 0.07 | 0.45 | 0.66 |
| *Stomach* | 0.949 | <0.0001 | 0.20 | 0.16 | 0.99 | 0.33 |
| *Intestine* | 0.932 | <0.0001 | 0.05 | 0.03 | 0.19 | 0.85 |
| Spleen | 0.939 | <0.0001 | 0.08 | -0.03 | -0.62 | 0.54 |
| Visceral organs | 0.934 | <0.0001 | 0.041 | 0.17 | 0.98 | 0.33 |
| **Non-Rodentia** | **N=24** | | | | | |
| Heart | 0.693 | 0.027 | 0.002 | 0.49 | 2.54 | **0.019** |
| Lungs | 0.781 | 0.002 | 0.009 | 0.01 | 0.50 | 0.96 |
| Kidneys | 0.768 | 0.002 | 0.003 | -0.14 | -0.72 | 0.48 |
| Liver | 0.78 | 0.001 | 0.007 | -0.08 | -0.49 | 0.63 |
| Digestive tract | 0.764 | 0.016 | 0.013 | -0.01 | -0.05 | 0.96 |
| *Stomach* | 0.824 | 0.005 | 0.10 | 0.11 | 0.53 | 0.60 |
| *Intestine* | 0.757 | 0.01 | 0.007 | -0.03 | -0.19 | 0.86 |
| Spleen | 0.827 | 0.0003 | 0.021 | -0.08 | -1.15 | 0.26 |
| Visceral organs | 0.768 | 0.003 | 0.004 | -0.02 | -0.10 | 0.92 |
| **Rodentia** | **N=21** | | | | | |
| Heart | 0.984 | 0.001 | 0.85 | 0.08 | 0.30 | 0.77 |
| Lungs | 0.995 | 0.001 | 0.95 | 0.15 | 0.57 | 0.57 |
| Kidneys | 1.000 | 0.0009 | 0.99 | 0.26 | 0.92 | 0.37 |
| Liver | 1.000 | 0.0004 | 1.00 | 0.25 | 1.77 | 0.09 |
| Digestive tract | 0.971 | 0.002 | 0.71 | -0.03 | -0.13 | 0.90 |
| *Stomach* | 0.974 | 0.001 | 0.74 | 0.002 | 0.006 | 0.99 |
| *Intestine* | 0.971 | 0.002 | 0.71 | -0.04 | -0.19 | 0.85 |
| Spleen | 0.972 | 0.001 | 0.72 | 0.02 | 0.26 | 0.80 |
| Visceral organs | 1.000 | 0.0008 | 1.00 | 0.40 | 1.61 | 0.12 |

**Supplementary Table 11:** Pair-wise phylogenetic least-squares regression (PGLS) between brain size and adipose depots mass, controlling for fat-free body mass minus brain mass. a) N=100 species, b) N=45 species.

| **a)** | | PGLS | | | | | | Independent contrasts (λ = 1) | | | Raw data (λ = 0) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value | β | t-value | p-value | β | t-value | p-value |
| Mammals | 100 | 0.939 | <0.0001 | 0.03 | -0.07 | -2.39 | **0.019** | | | | | | |
| Primates | 23 | 0.805 | *0.28* | *0.25* | -0.01 | -0.07 | 0.95 | -0.01 | -0.24 | 0.81 | -0.09 | -1.09 | 0.29 |
| Carnivora | 28 | 0.000 | 1.00 | 0.011 | -0.05 | -1.02 | 0.32 | | | | | | |
| Rodentia | 29 | 0.820 | <0.0001 | 0.010 | -0.08 | -1.95 | 0.06 | | | | | | |

| **b)** | | PGLS | | | | | |
|---|---|---|---|---|---|---|---|
| Group | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
| Mammals | 45 | 0.948 | <0.0001 | 0.20 | -0.11 | -2.84 | **0.007** |
| Rodentia | 24 | 0.826 | 0.0003 | 0.029 | -0.08 | -1.84 | **0.08** |
| Non-Rodentia | 21 | 0.934 | 0.0006 | 0.40 | -0.15 | -1.94 | **0.07** |

**Supplementary Table 12:** Results of a compositional data analysis between brain size, adipose depots mass and fat-free body mass. Pair-wise phylogenetic least-squares regression (PGLS) between the transformed variables. a) N=100 species, b) N=45 species.

| **a)** | | PGLS | | | | | |
|---|---|---|---|---|---|---|---|
| Group | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value |
| Mammals | 100 | 0.000 | 1.00 | <0.0001 | -0.64 | -8.21 | **<0.0001** |
| Primates | 23 | 0.766 | 0.033 | 0.021 | -0.57 | -5.78 | **<0.0001** |
| Carnivora | 28 | 0.000 | 1.00 | 0.0008 | -0.66 | -4.96 | **<0.0001** |
| Rodentia | 29 | 1.000 | <0.0001 | 1.00 | -0.80 | -9.19 | **<0.0001** |

| **b)** | | PGLS | | | | | | Raw data (λ = 0) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Group | N | λ | P (λ=0) | P (λ=1) | β | t-value | p-value | β | t-value | p-value |
| Mammals | 45 | 0.000 | 1.00 | <0.0001 | -0.80 | -6.78 | **<0.0001** | | | |
| Rodentia | 24 | 1.000 | *0.21* | *1.00* | -0.80 | -9.00 | **<0.0001** | -0.73 | -4.82 | **<0.0001** |
| Non-Rodentia | 21 | 0.000 | 1.00 | 0.0001 | -0.79 | -4.06 | **<0.0001** | | | |

### 3.6. The special case of primates

This section contains additional results on the relationship between brain size and adipose depots mass in primates, taking data quality into account.

Our hypothesis predicted that the negative correlation between brain size and adipose depots mass should also be present in primates as a group, but it was not (cf. Suppl. Table 4a). Even if the whole primate order would be following a cognitive buffering strategy in comparison to other mammalian taxa, we still expect that the relationship would be valid within the group, as not all primate species equally rely on cognitive buffering[15]. There are four reasons leading us to conclude that our data of primates do not accurately reflect the trade-off between adipose depots and brain size.

First, as our primate specimens were captives from a variety of husbandry conditions, there may be a large variation in fat storage in our sample which does not reflect "true" biological variation. Seasonality should be less of a concern for captive primates, but age and cause of death may strongly affect adipose depots in unpredictable directions. Indeed, many closely related species in our sample differ considerably in their amount of adipose depots. As tip contrasts have a large impact on the results of phylogenetic methods, they may mask an underlying trend (cf.[55]).

Second, Pond[13] reported that subcutaneous fat stores are more conspicuous in primates than in other groups, and we know from qualitative comparisons that different primate species store adipose depots at different places in their body. The small-brained fat-tailed dwarf lemurs (*Cheirogaleus medius* and *C. major*) store fat in their tails, increasing their body mass up to 78% before hibernation[56]. Orangutan males exhibit fatty cheek pads, and probably also store fat around the neck, in addition to abdominal fat stores[57]. Even within humans, males differ in fat store distribution from females[22]. Therefore, our measurements and subsequent scaling of abdominal fat stores may not be accurately estimating total body fat in some primate species, and the resulting error may mask any underlying correlation.

Third, peculiarities of the gastrointestinal tract of foregut fermenters may exert an influence on the capacity to store fat in captive animals. In the order of primates, only the subfamily Colobinae belongs to this group. In contrast to hindgut fermenters (i.e. all other primates), a diet of energy-dense, low-fiber foods does not increase body mass in this group, but rather leads to a loss of body mass, diarrhea, and premature death[58]. This is a well-known phenomenon in captive colobines, which are extremely sensitive to husbandry conditions and are

relatively rarely kept in zoos. Our sample contains two colobine species (*Colobus polykomos* and *Trachypithecus vetulus*). If these are excluded from the analysis, a very weak negative trend between brain size and adipose depots mass appears in the reduced sample (N=21, lambda =0.692, p-value of adipose depots on brain size controlling for body mass: 0.368, beta = -0.072).

Fourth, some of the primate specimens in our sample were rather light-weight in comparison to the wild adult body mass of the respective sex (<75%, *Cebus apella, Macaca nigra, Symphalangus syndactylus, Theropithecus gelada,* and *Mandrillus sphinx*). If we exclude these specimens from the analysis (in addition to the two colobines, see point 3), the negative trend between adipose depots and brain size, controlling for body mass, actually becomes significant (N=16, lambda =0.018, p =0.022, beta = -0.180). The same result is obtained by excluding only one single data point, *Cebus apella* (N=20, lambda =0, p-value of adipose depots on brain size controlling for body mass: 0.022, beta = -0.181). The latter species is represented by a single female individual of only 70% of the normal female body mass of this species. However, its adipose depots mass is, contrary to the overall low body mass, very high in comparison to other primates (51.4g abdominal fat mass, 1750g body mass). This leads to an extremely large contrast with its closest relative in our sample, a male *Saimiri boliviensis*, which exhibits a very low value of adipose depots mass (4.85g abdominal fat mass, 1003g body mass). But how can we know which of the two individuals is an outlier? For *Saimiri*, we have dissected two other specimens of a closely related species, *Saimiri sciureus*, which were not included in the final sample because their skull was damaged. All three *Saimiri* individuals exhibit a similarly low amount of abdominal adipose depots relative to body mass (less than 1% abdominal fat in all three specimens, as compared to 3% in the *Cebus apella*). It is therefore likely that the *Cebus apella* data point is an outlier, but we cannot say whether this is also found in other individuals of the species or genus or whether it is an abnormality of this specimen.

In conclusion, all four points taken together confirm that there is good reason to maintain that the negative correlation between adipose depots and brain size would also be found in primates, if more and more accurate data could be obtained. Obviously, we need more and more accurate data to settle this issue.

### 3.7. Costs of transporting adipose depots

This section contains a discussion of the energetic cost of transporting adipose depots in mammals, and a calculation of these costs in humans vs. chimpanzees.

Interspecifically, the metabolic cost of transport in animals increases with body mass, as demonstrated by Taylor et al.[59] for a wide range of animals. The cost of transport per gram body mass decreases with body mass$^{-0.33}$, and thus the cost of transport of the whole body increases with body mass$^{0.66}$. However, the relationship varies between orders or taxa groups, and there seems to be a steeper increase in rodents (N=15 species) and primates (N=10, including *Tupaia* and *Homo sapiens*) than in artiodactyls (N=10), carnivores (N=11) or marsupials (N=11)[59]. In any case, this interspecific relationship is likely to yield an underestimate of the metabolic cost of transport of additional adipose depots, as the musculoskeletal system does not grow in concert with additional body mass from fat storage.

Overall, the energy spent on locomotion varies widely between individuals of a species, depending on season, reproductive state, food availability and other variables. It can be estimated from day ranges and time spent on locomotion (cf.[16,60]), although day range is usually underestimating actual path length, which has a fractal dimension, and time spent on locomotion is confounded by the fact that some locomotion is also needed for other activities such as foraging or social life. Small animals of less than 500g body mass spend only about 1% of their total energy on locomotion, whereas this value increases to 5-15% in larger animals[16].

These values may seem to be rather small. However, the actual cost of carrying adipose depots may not only consist of an increase of the direct costs of locomotion, but in addition of an indirect cost of being less swift to escape predators. This cost depends on the lifestyle and may be higher in terrestrial and/or small species. Jumping distance is impaired in fatter cats[61], and in small monkeys forced to carry additional weights on their trunk[62]. Maximum running speed does not generally increase with body mass within taxa[63], and it even decreases in artiodactyls. In human athletes, the fastest and most enduring sportsmen are usually those with the lowest percentage of body fat, if training levels are also taken into account[64]. Therefore, it seems justified to assume that an increased percentage of adipose depots, without a parallel increase in the size of the musculoskeletal system, significantly decreases maximum running speeds also in animals.

Extant human foragers spend between 22% and 18% of their daily energy expenditure on locomotion (estimates of Leonard and Robertson[60], and of Isler and van Schaik[7] following a model of Pontzer and Wrangham[65]), and chimpanzees between 16% and 30% (same sources). Using the same equations, 10% additional fat stores would increase the percentage of energy used for locomotion about 1% in humans, but 2-3% in chimpanzees (the exact chimpanzee value differs according to whether we use the Taylor and Rowntree[66] equation for treadmill running of a juvenile chimpanzee (body mass 17kg), or the Taylor *et al.*[59] equation derived from 10 primate species).

Recently, Hanna and colleagues[67] have shown that vertical climbing efficiency increases only very slightly with body mass in primates (exponent of 0.11, not significantly different from zero), i.e. the cost of travel during climbing is almost directly proportional to body mass. We therefore expect that animals that include a fair amount of vertical travel are affected more strongly than predominantly terrestrial species by an increase in the size of adipose depots.

In conclusion, direct and indirect costs of adipose depots through their effect on locomotor efficiency are clearly evident, although they probably vary quite considerably between lineages or even more closely related species. Furthermore, available data and models confirm that the costs of quadrupedal locomotion and vertical climbing in nonhuman apes show a steeper increase with body mass than human walking or running. Efficient bipedalism similar to that of modern humans probably evolved in the first members of the genus *Homo* about 2 Ma ago[27]. Therefore, we conclude that storing fat would be less costly for an efficient biped such as early *Homo* than for their ancestors.

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**Supplementary dataset: Morphological and metabolic data**

N: number and sex of individuals for each species; Provenience: individual origin (captive or wild); $BM_{Org}$: body mass associated to organs masses; FFBM: fat-free body mass; Visc. mass: sum of all visceral organs; AD measure: abd=abdominal depots scaled to total by multiplication with 3.419 (see Methods), total=abdominal, subcutaneous and intermuscular depots; $BM_{BMR}$: body mass associated to basal metabolic rate; BMR: basal metabolic rate; Substitute species: c

| Order | Species | N | Provenience | Habitat | $BM_{Org}$ [g] | FFBM [g] | Brain mass [g] | Heart mass [g] | Lungs mass [g] | Kidneys mass [g] | Liver mass [g] | Digestive tract mass [g] | Stomach mass [g] | Intestine mass [g] | Spleen mass [g] | Visc. mass [g] | Adipose depots [g] | AD measure | $BM_{BMR}$ [g] | BMR [$mLO_2/h$] | Substitute species | Source BMR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Artiodactyla | *Capreolus capreolus* | 1f | Wild | Temperate | 20000.00 | 18358.88 | 100.00 | 160.00 | 260.00 | 80.00 | 480.00 | 1020.00 | 680.00 | 340.00 | 100.00 | 2100.00 | 1641.12 | abd | 20388.90 | 8161.20 | | 1 |
| Artiodactyla | *Gazella gazella* | 1f | Captive | Tropical | 15000.00 | 14702.17 | 79.25 | 119.98 | 349.32 | 40.59 | 326.91 | 587.12 | 364.77 | 222.35 | 33.66 | 1457.58 | 297.83 | abd | | | | |
| Artiodactyla | *Pudu puda* | 1m | Captive | Temperate | 12900.00 | 10340.88 | 61.64 | 50.48 | 102.98 | 19.92 | 205.73 | 153.05 | 112.13 | 40.92 | 61.81 | 593.97 | 2559.12 | abd | | | | |
| Carnivora | *Aonyx cinerea* | 3f/1m | Captive | Tropical | 2675.00 | 2504.55 | 35.94 | 15.14 | 40.61 | 30.55 | 106.42 | 45.40 | 11.42 | 33.98 | 18.74 | 256.86 | 170.45 | abd | | | | |
| Carnivora | *Arctictis binturong* | 1f/1m | Captive | Tropical | 10300.00 | 9954.63 | 60.48 | 75.19 | 240.16 | 51.33 | 915.18 | 239.70 | 83.88 | 155.82 | 20.68 | 1542.24 | 345.37 | abd | 14280.00 | 1128.10 | | 1 |
| Carnivora | *Canis lupus chango* | 2m | Captive | Temperate | 38000.00 | 32753.10 | 139.86 | 302.85 | 872.40 | 206.90 | 970.70 | 799.60 | 318.80 | 480.80 | 134.45 | 3286.90 | 5246.90 | total | 10550.00 | 3957.90 | | 1 |
| Carnivora | *Chrotagale owstoni* | 1f | Captive | Tropical | 1960.00 | 1909.36 | 23.31 | 11.58 | 21.53 | 12.79 | 44.05 | 60.46 | 17.19 | 43.27 | 4.91 | 155.32 | 50.64 | abd | | | | |
| Carnivora | *Cuon alpinus* | 1f/1m | Captive | Both | 20000.00 | 16434.19 | 116.29 | 157.79 | 263.22 | 76.41 | 346.22 | 265.90 | 110.25 | 155.65 | 54.53 | 1164.06 | 3565.81 | abd | | | | |
| Carnivora | *Felis chaus* | 1m | Captive | Both | 9800.00 | 8543.24 | 49.73 | 48.26 | 137.84 | 81.85 | 152.83 | 143.07 | 50.00 | 93.07 | 24.30 | 588.15 | 1256.76 | abd | | | | |
| Carnivora | *Felis silvestris* | 2f | Wild | Temperate | 2572.57 | 2429.16 | 38.07 | 10.33 | 25.74 | 15.35 | 50.17 | 101.08 | 21.40 | 79.69 | 3.69 | 206.36 | 143.40 | total | 2618.00 | 983.80 | | 10 |
| Carnivora | *Helogale parvula* | 1m | Captive | Tropical | 260.30 | 246.15 | 5.18 | 1.53 | 3.79 | 2.45 | 11.05 | 7.43 | 3.02 | 4.41 | 0.88 | 27.13 | 14.15 | abd | | | | |
| Carnivora | *Leopardus geoffroyi* | 1f | Captive | Both | 3100.00 | 2498.91 | 32.12 | 16.03 | 34.27 | 30.66 | 58.43 | 53.75 | 18.10 | 35.65 | 23.86 | 217.00 | 601.09 | abd | | | | |
| Carnivora | *Lontra canadensis* | 1f | Captive | Temperate | 7900.00 | 7570.48 | 42.48 | 54.05 | 309.58 | 74.72 | 255.00 | 109.48 | 24.26 | 85.22 | 73.79 | 876.62 | 329.52 | abd | | | | |
| Carnivora | *Lutra lutra* | 2f | Wild | Temperate | 5325.00 | 4859.69 | 47.79 | 51.37 | 142.04 | 61.06 | 254.64 | 120.66 | 33.05 | 87.61 | 27.32 | 777.73 | 465.31 | abd | 8671.40 | 4813.30 | | 1 |
| Carnivora | *Lutrogale perspicillata* | 1f | Captive | Tropical | 5100.00 | 4922.25 | 62.16 | 48.47 | 101.29 | 48.45 | 152.09 | 127.94 | 40.27 | 87.67 | 12.71 | 490.95 | 177.75 | abd | | | | |
| Carnivora | *Lynx canadensis* | 1f | Captive | Temperate | 10000.00 | 9165.32 | 82.62 | 38.81 | 93.78 | 54.91 | 157.87 | 171.01 | 63.89 | 107.12 | 8.00 | 524.38 | 834.68 | abd | 9400.00 | 4220.60 | *L. rufus* | 1 |
| Carnivora | *Lynx lynx* | 1f | Captive | Temperate | 17500.00 | 12860.42 | 94.28 | 92.70 | 206.70 | 79.50 | 263.50 | 321.50 | 137.50 | 184.00 | 26.00 | 989.90 | 4639.58 | abd | | | | |
| Carnivora | *Martes foina* | 3f/5m | Wild | Temperate | 1406.36 | 1363.52 | 19.03 | 9.80 | 20.07 | 7.34 | 34.87 | 46.62 | 14.56 | 32.06 | 5.48 | 124.18 | 42.85 | total | | | | |
| Carnivora | *Martes martes* | 1f/2m | Wild | Temperate | 1603.33 | 1540.08 | 20.46 | 10.85 | 22.83 | 8.79 | 37.89 | 33.08 | 13.21 | 19.87 | 3.00 | 116.44 | 63.25 | abd | 920.00 | 752.10 | | 1 |
| Carnivora | *Martes pennanti* | 1m | Wild | Temperate | 4790.00 | 4625.10 | 41.20 | 27.40 | 53.30 | 21.10 | 112.80 | 127.60 | 39.80 | 87.80 | 0.40 | 342.60 | 164.90 | total | | | | |
| Carnivora | *Mephitis mephitis* | 1f | Captive | Temperate | 1449.20 | 1117.56 | 9.84 | 6.00 | 17.60 | 6.62 | 17.41 | 38.69 | 10.49 | 28.20 | 4.65 | 90.97 | 331.64 | total | 5667.00 | 1507.50 | | 2 |
| Carnivora | *Mustela erminea* | 1m | Wild | Temperate | 258.84 | 253.34 | 5.70 | 2.47 | 4.40 | 2.34 | 9.98 | 7.16 | 1.80 | 5.36 | 0.91 | 27.26 | 5.50 | total | 207.50 | 329.80 | | 1 |
| Carnivora | *Mustela nivalis* | 1f | Wild | Temperate | 32.36 | 30.97 | 1.81 | 0.36 | 0.53 | 0.43 | 1.55 | 1.22 | 0.33 | 0.89 | 0.12 | 4.21 | 1.39 | total | 80.60 | 186.10 | | 1 |
| Carnivora | *Mustela putorius* | 1m | Wild | Temperate | 640.00 | 582.22 | 10.36 | 4.80 | 12.80 | 4.00 | 28.80 | 21.10 | 6.50 | 14.60 | 3.60 | 75.10 | 57.78 | abd | 1466.70 | 1260.80 | | 1 |
| Carnivora | *Panthera tigris altaica* | 1m | Captive | Temperate | 75000.00 | 74042.41 | 341.88 | 304.97 | 1042.50 | 424.57 | 1103.50 | 1691.82 | 608.90 | 1082.92 | 68.19 | 4635.55 | 957.59 | abd | 137900.00 | 23994.60 | | 1 |
| Carnivora | *Potos flavus* | 1m | Captive | Tropical | 3920.00 | 3060.97 | 31.08 | 21.05 | 49.06 | 14.40 | 165.72 | 56.06 | 17.56 | 38.50 | 11.23 | 317.52 | 859.03 | total | 2406.00 | 803.70 | | 1 |
| Carnivora | *Prionailurus viverrinus* | 1f | Captive | Tropical | 7300.00 | 6342.68 | 52.92 | 33.46 | 110.75 | 55.88 | 159.93 | 202.00 | 91.63 | 110.37 | 16.22 | 578.24 | 957.32 | abd | | | | |
| Carnivora | *Proteles cristata* | 1m | Captive | Tropical | 5400.00 | 5242.42 | 39.89 | 90.57 | 142.91 | 24.31 | 181.82 | 154.65 | 69.95 | 84.70 | 28.74 | 623.00 | 157.58 | abd | 7928.20 | 2013.50 | | 1 |
| Carnivora | *Puma yagouaroundi* | 1m | Captive | Tropical | 5900.00 | 4623.58 | 42.99 | 29.62 | 70.37 | 39.13 | 115.57 | 98.98 | 47.24 | 51.74 | 15.52 | 369.19 | 1276.42 | abd | 6105.00 | 1556.80 | | 1 |
| Carnivora | *Vulpes corsac* | 1f/1m | Captive | Temperate | 2075.00 | 1753.20 | 34.06 | 21.69 | 41.05 | 8.84 | 35.57 | 37.09 | 15.02 | 22.08 | 5.00 | 149.23 | 321.80 | abd | | | | |
| Carnivora | *Zalophus californianus* | 1f | Captive | Temperate | 34000.00 | 33311.93 | 309.76 | 168.11 | 785.30 | 205.85 | 1274.00 | 996.02 | 306.58 | 689.44 | 124.75 | 3554.03 | 688.07 | abd | 22700.00 | 8921.10 | | 1 |
| Chiroptera | *Lasionycteris noctivagans* | 1f | Wild | Temperate | 14.75 | 10.69 | 0.16 | 0.16 | 0.21 | 0.13 | 0.33 | 0.61 | 0.11 | 0.50 | 0.01 | 1.45 | 4.06 | total | | | | |
| Chiroptera | *Lasiurus borealis* | 1f | Wild | Temperate | 13.51 | 10.54 | 0.17 | 0.14 | 0.20 | 0.11 | 0.35 | 0.35 | 0.07 | 0.29 | 0.01 | 1.16 | 2.97 | total | 12.20 | 17.45 | | 3 |
| Chiroptera | *Nyctalus noctula* | 3m | Wild | Temperate | 25.64 | 23.75 | 0.32 | 0.37 | 0.55 | 0.13 | 0.46 | 0.83 | 0.24 | 0.59 | 0.06 | 2.40 | 1.89 | total | | | | |
| Didelphimorphia | *Didelphis virginiana* | 2f/2m | Wild | Temperate | 2633.50 | 2400.53 | 8.34 | 12.13 | 30.25 | 22.90 | 157.30 | 67.18 | 22.75 | 44.43 | 13.13 | 302.88 | 232.98 | total | 2488.30 | 800.90 | | 1 |
| Diprotodontia | *Macropus agilis* | 1m | Captive | Tropical | 7700.00 | 7608.71 | 30.82 | 60.15 | 117.66 | 46.34 | 202.66 | 242.30 | 151.44 | 90.86 | 18.46 | 687.57 | 91.29 | abd | 4913.10 | 1375.70 | *M. eugenii* | 1 |
| Diprotodontia | *Potorous tridactylus* | 1m | Captive | Temperate | 809.00 | 799.94 | 11.40 | 4.81 | 14.52 | 6.21 | 23.71 | 25.67 | 11.42 | 14.25 | 2.71 | 77.63 | 9.06 | abd | 1068.60 | 553.70 | | 1 |
| Diprotodontia | *Trichosurus vulpecula* | 1m | Captive | Tropical | 1550.00 | 1521.55 | 12.69 | 8.96 | 20.39 | 13.50 | 33.15 | 94.51 | 18.47 | 76.04 | 1.12 | 171.63 | 28.45 | abd | 1996.80 | 693.70 | | 1 |
| Eulipotyphla | *Blarina brevicauda* | 3f/2m | Wild | Temperate | 17.81 | 17.14 | 0.32 | 0.18 | 0.28 | 0.21 | 0.93 | 0.36 | 0.12 | 0.23 | 0.12 | 2.09 | 0.67 | total | 19.80 | 53.90 | | 1 |
| Eulipotyphla | *Crocidura russula* | 6f/1m | Wild | Temperate | 9.55 | 8.95 | 0.17 | 0.08 | 0.16 | 0.13 | 0.55 | 0.61 | 0.14 | 0.47 | 0.12 | 1.63 | 0.59 | total | 9.80 | 23.40 | | 1 |
| Eulipotyphla | *Erinaceus europaeus* | 1f/1m | Wild | Temperate | 949.55 | 855.58 | 4.30 | 5.50 | 15.70 | 8.94 | 49.62 | 48.84 | 11.30 | 37.54 | 5.48 | 134.07 | 93.97 | total | 936.70 | 360.90 | | 1 |
| Eulipotyphla | *Neomys anomalus* | 1f | Wild | Temperate | 10.28 | 9.90 | 0.25 | 0.15 | 0.29 | 0.22 | 1.12 | 0.46 | 0.08 | 0.38 | 0.28 | 2.52 | 0.38 | total | 13.40 | 66.80 | | 1 |
| Eulipotyphla | *Neomys fodiens* | 1f | Wild | Temperate | 15.69 | 14.58 | 0.25 | 0.14 | 0.24 | 0.22 | 0.55 | 0.65 | 0.15 | 0.50 | 0.14 | 1.94 | 1.11 | total | 15.90 | 49.80 | | 1 |
| Eulipotyphla | *Sorex araneus* | 1m | Wild | Temperate | 7.51 | 7.20 | 0.15 | 0.11 | 0.07 | 0.11 | 0.38 | 0.43 | 0.11 | 0.32 | 0.08 | 1.18 | 0.31 | total | 8.20 | 43.10 | | 1 |
| Eulipotyphla | *Talpa europaea* | 5m | Wild | Temperate | 51.35 | 49.64 | 1.00 | 0.31 | 0.65 | 0.36 | 1.52 | 1.99 | 0.62 | 1.37 | 0.23 | 5.08 | 1.71 | total | | | | |
| Lagomorpha | *Lepus europaeus* | 1m | Wild | Temperate | 3338.70 | 3196.30 | 14.76 | 28.94 | 37.69 | 18.46 | 90.41 | 115.74 | 15.35 | 100.39 | 1.18 | 292.42 | 142.40 | total | | | | |
| Lagomorpha | *Sylvilagus floridanus* | 6f/1m | Wild | Temperate | 971.71 | 958.36 | 7.89 | 4.79 | 12.15 | 6.25 | 31.99 | 44.72 | 7.50 | 37.22 | 0.59 | 100.50 | 13.36 | total | | | | |
| Primates | *Alouatta sara* | 1f | Captive | Tropical | 4400.00 | 4325.71 | 56.46 | 24.00 | 47.63 | 9.86 | 81.21 | 113.35 | 32.21 | 81.14 | 6.17 | 282.22 | 74.29 | abd | 4670.00 | 2000.30 | *A. palliata* | 1 |
| Primates | *Callithrix jacchus* | 1m | Captive | Tropical | 311.60 | 306.06 | 7.25 | 2.83 | 4.66 | 2.94 | 17.84 | 10.80 | 1.39 | 9.41 | 0.54 | 39.61 | 5.54 | abd | 190.00 | 157.70 | | 1 |
| Primates | *Cebuella pygmaea* | 1f | Captive | Tropical | 163.00 | 141.05 | 4.40 | 0.86 | 1.86 | 1.91 | 13.49 | 6.96 | 0.76 | 6.20 | 0.18 | 25.26 | 21.95 | abd | 140.60 | 99.80 | | 1 |
| Primates | *Cebus apella* | 1f | Captive | Tropical | 1750.00 | 1574.30 | 50.76 | 13.38 | 29.30 | 10.40 | 49.28 | 44.41 | 7.98 | 36.43 | 1.25 | 148.02 | 175.70 | abd | | | | |
| Primates | *Cheirogaleus medius* | 1f | Captive | Tropical | 231.00 | 216.91 | 2.83 | 0.93 | 1.75 | 1.00 | 6.31 | 3.78 | 1.31 | 2.47 | 0.32 | 14.09 | 14.09 | abd | 329.80 | 195.90 | | 1 |
| Primates | *Chlorocebus pygerythrus* | 1m | Captive | Tropical | 5300.00 | 5060.50 | 80.81 | 42.58 | 65.46 | 12.11 | 88.67 | 74.06 | 21.69 | 52.37 | 3.74 | 286.62 | 239.50 | abd | | | | |
| Primates | *Colobus guereza* | 1f/1m | Captive | Tropical | 9750.00 | 9561.58 | 86.51 | 36.97 | 128.45 | 23.25 | 171.33 | 302.35 | 188.91 | 113.44 | 7.25 | 669.60 | 188.42 | abd | 10450.00 | 2978.30 | | 1 |
| Primates | *Eulemur fulvus fulvus* | 1m | Captive | Tropical | 2500.00 | 2115.36 | 22.53 | 11.80 | 27.17 | 9.52 | 43.37 | 41.21 | 8.26 | 32.95 | 1.90 | 134.97 | 384.64 | abd | 2330.00 | 324.80 | | 1 |
| Primates | *Eulemur macaco macaco* | 2m | Captive | Tropical | 1875.00 | 1726.07 | 24.22 | 9.14 | 26.26 | 14.16 | 77.78 | 53.98 | 13.14 | 40.85 | 11.70 | 193.02 | 148.93 | abd | | | | |
| Primates | *Hylobates concolor* | 1f | Captive | Tropical | 6550.00 | 6475.67 | 137.79 | 58.19 | 135.64 | 35.21 | 293.00 | 344.53 | 94.10 | 250.43 | 25.45 | 892.02 | 74.33 | abd | | | | |
| Primates | *Lemur catta* | 1f/1m | Captive | Tropical | 2075.00 | 1864.80 | 22.79 | 11.66 | 24.37 | 11.20 | 72.90 | 67.81 | 16.70 | 51.11 | 2.27 | 190.20 | 210.20 | abd | 2678.00 | 389.00 | | 9 |
| Primates | *Leontopithecus chrysomelas* | 3m | Captive | Tropical | 641.67 | 586.16 | 13.21 | 3.82 | 8.61 | 4.13 | 18.92 | 15.01 | 3.71 | 11.30 | 1.10 | 51.60 | 55.50 | abd | 733.00 | 382.00 | *L. rosalia* | 4 |
| Primates | *Macaca arctoides* | 3m | Captive | Tropical | 15866.67 | 14187.56 | 118.02 | 60.76 | 123.38 | 49.95 | 240.82 | 246.02 | 68.34 | 177.68 | 11.36 | 732.28 | 1679.11 | abd | | | | |
| Primates | *Macaca nigra* | 1m | Captive | Tropical | 5600.00 | 5267.50 | 105.15 | 23.93 | 47.01 | 18.64 | 94.86 | 178.32 | 39.37 | 138.95 | 10.10 | 372.86 | 332.50 | abd | 6060.00 | 2273.20 | *M. mulatta* | 1 |
| Primates | *Mandrillus sphinx* | 1m | Captive | Tropical | 23000.00 | 20667.90 | 167.83 | 75.77 | 180.97 | 49.87 | 330.52 | 436.70 | 121.34 | 315.36 | 12.24 | 1086.07 | 2332.10 | abd | | | | |
| Primates | *Papio hamadryas* | 2m | Captive | Tropical | 23250.00 | 22243.17 | 173.92 | 103.16 | 253.56 | 80.31 | 392.02 | 458.67 | 86.42 | 372.25 | 26.78 | 1314.48 | 1006.83 | abd | 15900.00 | 5066.60 | *Papio ursinus* | 1 |
| Primates | *Saguinus fuscicollis lagonotus* | 1m | Captive | Tropical | 330.00 | 318.82 | 7.77 | 3.30 | 3.84 | 1.93 | 14.35 | 9.66 | 1.31 | 8.35 | 0.36 | 33.44 | 11.18 | abd | | | | |
| Primates | *Saguinus oedipus* | 1f/1m | Captive | Tropical | 624.00 | 560.80 | 9.97 | 3.68 | 7.45 | 3.15 | 20.89 | 12.67 | 2.35 | 10.32 | 0.33 | 48.15 | 63.20 | abd | 296.00 | 265.50 | | 1 |
| Primates | *Saimiri boliviensis* | 1m | Captive | Tropical | 1003.00 | 986.42 | 29.01 | 6.47 | 7.80 | 6.70 | 19.43 | 25.30 | 5.95 | 19.35 | 1.09 | 66.79 | 16.58 | abd | 850.00 | 592.00 | | 5 |
| Primates | *Symphalangus syndactylus* | 1m | Captive | Tropical | 8500.00 | 7913.40 | 142.97 | 51.45 | 115.79 | 43.72 | 293.72 | 406.85 | 138.46 | 268.39 | 22.71 | 934.24 | 586.60 | abd | | | | |
| Primates | *Theropithecus gelada* | 1m | Captive | Tropical | 11400.00 | 10938.30 | 140.90 | 77.22 | 173.87 | 38.04 | 235.52 | 361.45 | 51.94 | 309.51 | 9.31 | 895.41 | 461.70 | abd | | | | |
| Primates | *Trachypithecus vetulus* | 1f | Captive | Tropical | 5000.00 | 3876.04 | 72.00 | 19.16 | 60.59 | 15.41 | 90.42 | 150.81 | 107.24 | 43.57 | 2.85 | 339.24 | 1123.96 | abd | | | | |
| Primates | *Varecia rubra* | 1f | Captive | Tropical | 4200.00 | 3135.22 | 35.74 | 18.11 | 39.57 | 22.41 | 72.22 | 82.57 | 29.29 | 53.28 | 4.49 | 239.37 | 1064.78 | abd | 3512.00 | 603.00 | *V.variegata* | 9 |
| Rodentia | *Acomys minous* | 1m | No data | Temperate | 42.47 | 40.13 | 0.90 | 0.18 | 0.34 | 0.32 | 0.93 | 1.10 | 0.38 | 0.72 | 0.07 | 2.94 | 2.34 | total | | | | |
| Rodentia | *Agouti paca* | 1m | Captive | Tropical | 5460.00 | 5407.50 | 32.12 | 17.57 | 41.34 | 22.17 | 140.13 | 110.31 | 17.75 | 92.56 | 6.31 | 337.83 | 52.50 | total | 6831.50 | 2364.90 | | 1 |
| Rodentia | *Apodemus flavicollis* | 3f/1m | Wild | Temperate | 25.04 | 24.51 | 0.61 | 0.18 | 0.36 | 0.34 | 0.99 | 1.35 | 0.27 | 1.08 | 0.07 | 3.28 | 0.54 | total | 23.40 | 42.40 | | 1 |
| Rodentia | *Apodemus sylvaticus* | 1f/1m | Wild | Temperate | 18.28 | 17.38 | 0.57 | 0.14 | 0.24 | 0.26 | 1.10 | 1.20 | 0.25 | 0.96 | 0.06 | 2.99 | 0.90 | total | 20.90 | 55.90 | | 1 |
| Rodentia | *Arvicola terrestris* | 2m | Wild | Temperate | 61.81 | 60.09 | 1.05 | 0.28 | 0.50 | 0.70 | 2.58 | 3.78 | 0.89 | 2.90 | 0.08 | 7.92 | 1.72 | total | | | | |
| Rodentia | *Castor fiber* | 3m | Wild | Temperate | 15563.05 | 13497.32 | 48.86 | 43.90 | 138.16 | 78.33 | 345.11 | 439.55 | 103.45 | 336.10 | 6.10 | 1051.15 | 2065.73 | total | | | | |
| Rodentia | *Dasyprocta azarae* | 1f | Captive | Tropical | 4100.00 | 4041.06 | 23.83 | 30.42 | 41.71 | 22.69 | 93.47 | 105.83 | 21.85 | 83.98 | 3.93 | 298.05 | 58.94 | abd | 3849.00 | 1886.00 | | 1 |
| Rodentia | *Dasyprocta punctata* | 1m | Captive | Tropical | 3400.00 | 3293.81 | 22.79 | 36.34 | 36.25 | 21.29 | 108.84 | 138.82 | 21.75 | 117.07 | 2.75 | 344.29 | 106.19 | abd | | | | |
| Rodentia | *Dolichotis patagonum* | 1m | Captive | Temperate | 8430.00 | 8133.54 | 36.52 | 65.05 | 153.34 | 36.01 | 158.22 | 153.11 | 26.25 | 126.86 | 11.56 | 577.29 | 296.46 | abd | 1613.00 | 725.90 | *D. salinicola* | 1 |
| Rodentia | *Gerbillus perpallidus* | 1f/1m | Captive | Temperate | 30.05 | 26.39 | 0.58 | 0.13 | 0.23 | 0.27 | 0.97 | 0.85 | 0.32 | 0.53 | 0.12 | 2.55 | 3.66 | total | 72.90 | 65.00 | | 1 |
| Rodentia | *Glaucomys volans* | 2f/1m | Wild | Both | 55.10 | 54.03 | 1.85 | 0.56 | 0.90 | 0.59 | 2.90 | 1.94 | 0.42 | 1.52 | 0.21 | 7.10 | 1.07 | total | 64.00 | 64.20 | | 1 |
| Rodentia | *Glis glis* | 1f/2m | Wild | Temperate | 83.41 | 64.77 | 1.54 | 0.48 | 0.87 | 0.68 | 3.18 | 2.20 | 0.65 | 1.55 | 0.12 | 7.52 | 18.64 | total | 151.30 | 92.29 | | 6 |
| Rodentia | *Hydrochaeris hydrochaeris* | 1m | Captive | Tropical | 34000.00 | 32343.43 | 83.92 | 104.20 | 390.30 | 103.48 | 696.10 | 751.14 | 80.61 | 670.53 | 36.65 | 2081.87 | 1656.57 | abd | 26400.00 | 6600.00 | | 1 |
| Rodentia | *Hystrix indica* | 2m | Captive | Tropical | 11250.00 | 10866.68 | 40.66 | 56.16 | 151.79 | 52.38 | 255.19 | 395.07 | 102.52 | 292.55 | 27.50 | 938.07 | 383.32 | abd | 11066.70 | 2568.20 | *H. africaeaustralis* | 1 |
| Rodentia | *Jaculus jaculus* | 1f | Captive | Tropical | 47.92 | 44.73 | 1.20 | 0.45 | 0.79 | 0.29 | 1.12 | 1.61 | 0.25 | 1.36 | 0.09 | 4.35 | 3.19 | total | 109.70 | 106.40 | | 1 |
| Rodentia | *Microtus agrestis* | 3f/6m | Wild | Temperate | 15.49 | 14.98 | 0.39 | 0.12 | 0.23 | 0.17 | 0.63 | 1.23 | 0.25 | 0.98 | 0.04 | 2.43 | 0.51 | total | 28.00 | 63.60 | | 7 |
| Rodentia | *Microtus arvalis* | 1m | Wild | Temperate | 27.00 | 25.52 | 0.39 | 0.19 | 0.44 | 0.55 | 1.87 | 1.88 | 0.32 | 1.56 | 0.30 | 5.23 | 1.48 | total | 20.30 | 51.20 | | 1 |
| Rodentia | *Microtus pinetorum* | 1f | Wild | Temperate | 20.96 | 20.60 | 0.58 | 0.15 | 0.24 | 0.36 | 1.15 | 1.29 | 0.34 | 0.95 | 0.04 | 3.22 | 0.36 | total | 24.10 | 52.50 | | 1 |
| Rodentia | *Mus musculus* | 1f | Wild | Temperate | 14.93 | 14.83 | 0.36 | 0.07 | 0.14 | 0.28 | 0.68 | 0.78 | 0.19 | 0.59 | 0.03 | 1.98 | 0.11 | total | 22.60 | 57.30 | | 1 |
| Rodentia | *Myodes glareolus* | 1m | Wild | Temperate | 15.49 | 15.05 | 0.35 | 0.10 | 0.24 | 0.24 | 0.67 | 1.17 | 0.25 | 0.92 | 0.05 | 2.47 | 0.44 | total | 20.80 | 67.10 | | 1 |
| Rodentia | *Octodon degus* | 2m | Captive | Temperate | 129.36 | 116.97 | 1.90 | 0.41 | 1.13 | 1.14 | 4.80 | 3.59 | 0.79 | 2.81 | 0.48 | 11.54 | 12.39 | total | 237.50 | 201.30 | | 1 |
| Rodentia | *Ondatra zibethicus* | 1f/3m | Wild | Temperate | 991.00 | 947.03 | 4.71 | 3.00 | 8.55 | 5.78 | 25.98 | 32.45 | 6.70 | 25.75 | 0.28 | 76.03 | 43.98 | total | 879.50 | 679.50 | | 1 |
| Rodentia | *Peromyscus leucopus* | 1f | Wild | Both | 22.12 | 21.38 | 0.74 | 0.15 | 0.18 | 0.30 | 1.23 | 0.87 | 0.30 | 0.57 | 0.02 | 2.75 | 0.75 | total | 22.40 | 109.50 | | 1 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rodentia | *Rattus norvegicus* | 3f/3m | No data | Temperate | 209.91 | 190.99 | 2.32 | 0.87 | 2.37 | 1.54 | 9.16 | 6.88 | 1.54 | 5.34 | 1.22 | 22.04 | 18.92 | total | 289.50 | 307.50 | | 1 |
| Rodentia | *Rhabdomys pumilio* | 1f/4m | Captive | Tropical | 50.27 | 43.28 | 0.59 | 0.21 | 0.37 | 0.41 | 1.84 | 1.55 | 0.42 | 1.13 | 0.12 | 4.50 | 7.00 | total | 53.70 | 47.80 | | 1 |
| Rodentia | *Sciurus carolinensis* | 5f/2m | Wild | Temperate | 595.76 | 536.09 | 7.47 | 2.81 | 7.14 | 3.24 | 16.41 | 10.87 | 3.04 | 7.83 | 1.30 | 41.79 | 59.67 | total | 440.00 | 369.60 | | 1 |
| Rodentia | *Sciurus niger* | 2f | Wild | Temperate | 412.40 | 401.50 | 7.46 | 2.50 | 4.05 | 3.00 | 10.70 | 9.55 | 3.10 | 6.45 | 0.80 | 30.60 | 10.90 | total | | | | |
| Rodentia | *Sciurus vulgaris* | 1f/3m | Wild | Temperate | 274.55 | 271.80 | 6.28 | 1.68 | 3.21 | 1.70 | 5.53 | 8.34 | 1.84 | 6.51 | 0.30 | 20.75 | 2.75 | total | | | | |
| Rodentia | *Tamias striatus* | 2f/1m | Wild | Temperate | 103.97 | 100.49 | 2.36 | 0.66 | 1.53 | 0.81 | 2.94 | 3.09 | 0.48 | 2.62 | 0.25 | 9.27 | 3.48 | total | 97.20 | 120.30 | | 1 |
| Scandentia | *Tupaia glis* | 1m | Captive | Tropical | 140.80 | 137.76 | 3.44 | 1.17 | 1.70 | 1.13 | 3.39 | 2.12 | 1.04 | 1.08 | 0.01 | 9.52 | 3.04 | abd | 123.00 | 93.50 | | 8 |

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lose-related species with available BMR.